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63, line 23, *for* (O. F. Muell.) Schrank *read* (Schrank), O. F. Muell.
66, „ 23, *for* Bacillariæ *read* Bacillarieæ.
95, „ 35, for *Perdinium* read *Peridinium.*
115, „ 9, for *Psychophyton* read *Psychrophyton.*
123, „ 28, for *Amrrica* read *America.*
134, „ 10, for *H. triflora* read *C. triflora.*
180, „ 16 from bottom, *for* développent *read* développement.
225, „ 1, for *G. brachiatum* read *C. brachiatum.*
258, „ 2 from bottom, for *Vernonicæ* read Vernonieæ.
281, „ 3, for *mirocephalum* read *microcephalum.*
281, „ 16, *for* broa *read* broad.
427, „ 7, *for* 1923 *read* 1922.
428, „ 4, *for* aud *read* and.
428, „ 2 from bottom, *for* This *read* A.
431, „ 24, *for* nt *read* ut.
442, „ 3 from bottom, for *Gaditanæ* read *gaditanæ.*
455, „ 2, *for* minor *read* minores.
461, „ 14, *add, after* d'Alger: No. 184.
462, „ 10, *for* corolla *read* corollâ.
465, „ 11, *for* descriptien *read* description.
469, „ 4, *for* officinalis *Pugs. read* officinalis *Linn.*
469, „ 27, *for* Caroliana *Pugs. read* Caroliana *Pugs.**.
485, „ 10 from bottom, *for* Umbellifloræ *read* Umbelliferæ.
512, „ 22, *for* The artist *read* The botanist.
519, „ 11, for *hemaphrodita* read *hermaphrodita.*

THE JOURNAL

OF

THE LINNEAN SOCIETY.

(BOTANY.)

# Leaf and Stem Anatomy of *Tradescantia fluminensis*, Vell.

By Lorna I. Scott, B.Sc., and J. H. Priestley, D.S.O., B.Sc., F.L.S., Department of Botany. University of Leeds.

(With 10 Text-figures.)

[Read 19th June, 1924.]

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## I. Introduction.

The present paper is the result of the authors' perplexity as to the manner in which the Monocotyledon leaf type combines its method of growth with the necessary free access of sap to the growing lamina. The Monocotyledon leaf lamina is described as typically growing by a basal meristem as compared with the marginal one of many Dicotyledons, and, in such long-leaved types as *Iris* or in the palms, the activity of this basal meristem must be extensive and long-continued. A recent experimental study of the tissues of growing points (24) has led to the conclusion that meristematic tissue usually presents considerable resistance to the flow of sap, when the question naturally arises as to how the area of the Monocotyledon leaf, beyond the basal meristem, is nourished. The vascular bundles may penetrate the meristem at a very early date, though it is difficult to obtain precision upon this point from the literature, and in the case of the palm leaf some published descriptions certainly suggest that the whole of the base of the lamina remains meristematic. If the vein penetrates the meristem at an early period in its development, the problem still remains as to how the new tracheal elements are to be inserted in the vascular strands if leaf-growth takes place entirely from the base.

When this problem was first visualized, the literature accessible seemed to provide no clue to its solution. A paper by Buchholz (**3**), in which the same question initiated the investigation, was not seen until the present paper was written, and it is interesting to note along what different lines this author's work has developed from the same starting-point. In both cases the work began by an examination of a number of leaf types, but it soon became clear to the present writers that its solution necessitated a continuous developmental study. The original problem has been to some extent solved for this particular type, but still remains of interest for the vascular anatomy of the Monocotyledon in general. The investigation has also led to a re-examination of certain problems presented by the anatomy and foliar development of *Tradescantia*, and it is hoped that some light may be thrown upon certain features, which, whilst characteristic of *Tradescantia*, are also common to many other Monocotyledons, viz.:—

(1) The inter-relation of the vascular system of stem and leaf.

(2) The characteristic ring of the sclerenchyma within the outer cortex.

(3) The closed type of venation and the entire leaf margin, and their relation to the method of growth of the lamina.

(4) The different effect of etiolation conditions upon the Monocotyledon as compared with the typical Dicotyledon.

## II. STEM ANATOMY.

*Tradescantia fluminensis*, Vell., is a common greenhouse plant with a slender, trailing, branched stem, which is attached to the soil by means of adventitious roots from the older nodes. In transverse section of a mature internode (fig. 1), a cortical region is marked off from the medullary by a sclerenchymatous sheath, in which is embedded the outer ring of bundles (**8**, p. 101). The cortical region is bounded by a small-celled epidermis, and consists of a few layers of collenchyma and the assimilating parenchyma of the stem. The medullary region consists of large-celled parenchyma, in which are embedded numerous vascular bundles, which differ from those of the external ring in the absence of any thickened sheath. The sequence and manner of development of the bundles of the stem show that they fall very naturally into series, which for convenience in further discussion will be referred to under the following names:—

(1) *Medullary bundles.*

An inner ring of 3–6 bundles.

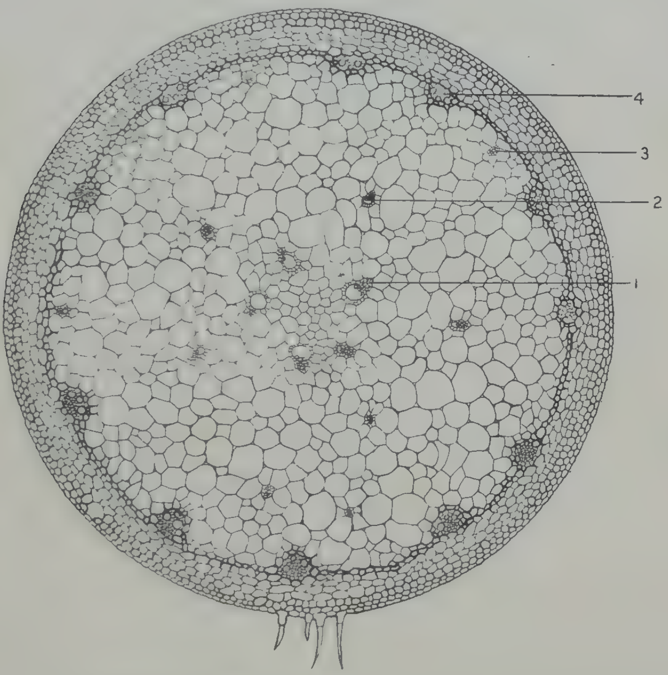
"Anastomotiques internes." (Gravis, **8**, p. 63.)

(2) *Perimedullary.*

A ring of 6–7 bundles, roughly alternating with the medullary. These bundles are not all equidistant from the centre of the stem, the larger ones being nearer the centre.

"Foliaires ou sortants." (**8**, p. 63.)

FIG. 1.



Transverse section of a mature internode. (× 25.)

1. Medullary bundle.
2. Perimedullary bundle.
3. Cortical bundle.
4. Peripheral bundle.

(3) *Cortical.*

A few small bundles, variable in number, which occur just inside the sclerenchymatous sheath, and where present alternate with the bundles of the outermost ring.

"Foliaires ou sortants." (**8**.)

(4) *Peripheral.*

A ring of about 12 bundles, embedded in the sclerenchymatous sheath.

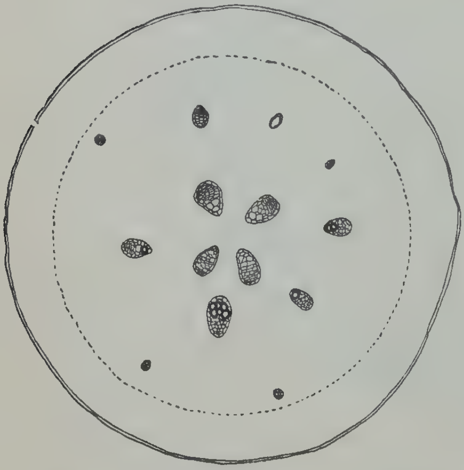
"Anastomotiques externes." (**8**.)

At the nodes the bundles of the different series are in connection, the medullary and perimedullary bundles fusing to form a central mass, and the peripheral to form a ring—these two masses being also connected by anastomosing strands of vascular tissue.

## III. The Development of the Vascular System.

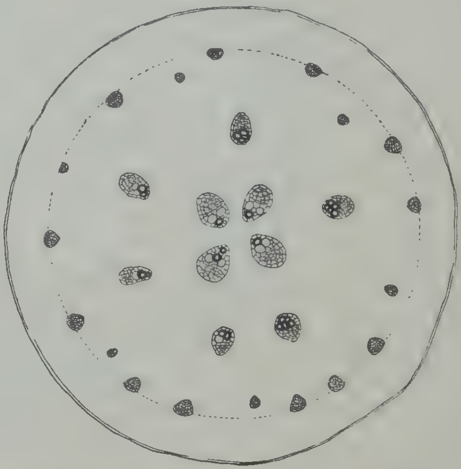
In studying the development of *Tradescantia*, the vascular systems of stem and leaf are found to be so closely inter-related that it is difficult to obtain a clear idea of the sequence of events without considering the two together. At any one level of the stem, the perimedullary bundles are the first to show lignified xylem. In fig. 2 *a* a transverse section of the stem is shown at an early stage of differentiation, when only the three median perimedullary bundles show lignified xylem, and in fig. 2 *b* a section of the internode below shows lignified xylem in all the perimedullary bundles and to a less extent in the medullary. At this stage the cortical and peripheral bundles are represented merely by procambial strands. This order of development is further exemplified by the longitudinal course of the bundles. The medullary bundles run the length of one internode, at the upper extremity of which they fuse, the spiral vessels of the bundles being replaced by the short irregular tracheids of the nodal mass. A re-distribution of material takes place to left and right of the original bundles, with the result that the bundles which emerge above the node and run up the second internode in the perimedullary position roughly alternate with the medullary bundles of the first internode, with the exception of the median, which is an almost direct continuation of one of the medullary bundles. In this second internode, later in development, bundles appear in the medullary position (fig. 3) (**4**, p. 269).

Fig. 2 *a*.



Transverse section of a young internode, showing xylem differentiated in the perimedullary bundles. (About 190 μ below shoot apex) (× 80).

Fig. 2 *b*.



Transverse section of a young internode, showing xylem differentiated in the perimedullary and medullary bundles. (About 230 μ below shoot apex) (× 60). Internode below text-fig. 2 *a*.

The bundles pass up one internode in the perimedullary position, and then pass out as the leaf-trace and form the primary longitudinal veins of the leaf. The median bundle enters the base of the leaf rather earlier than the more lateral leaf-trace bundles. This stage is reached very early in the development of the leaf, the protoxylem of the median bundle being distinguishable in the base of the lamina, when the latter is only 1–2 mm. in

Fig. 3.

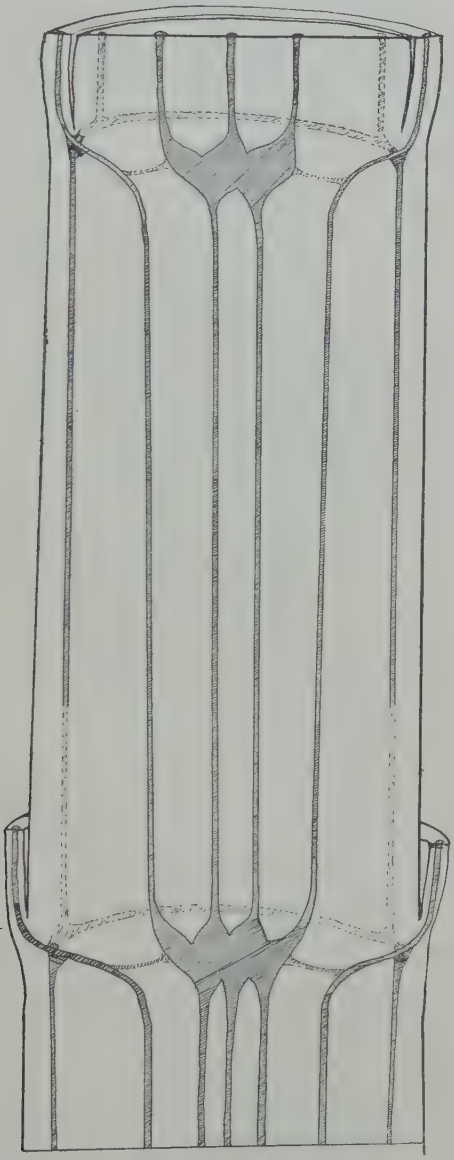
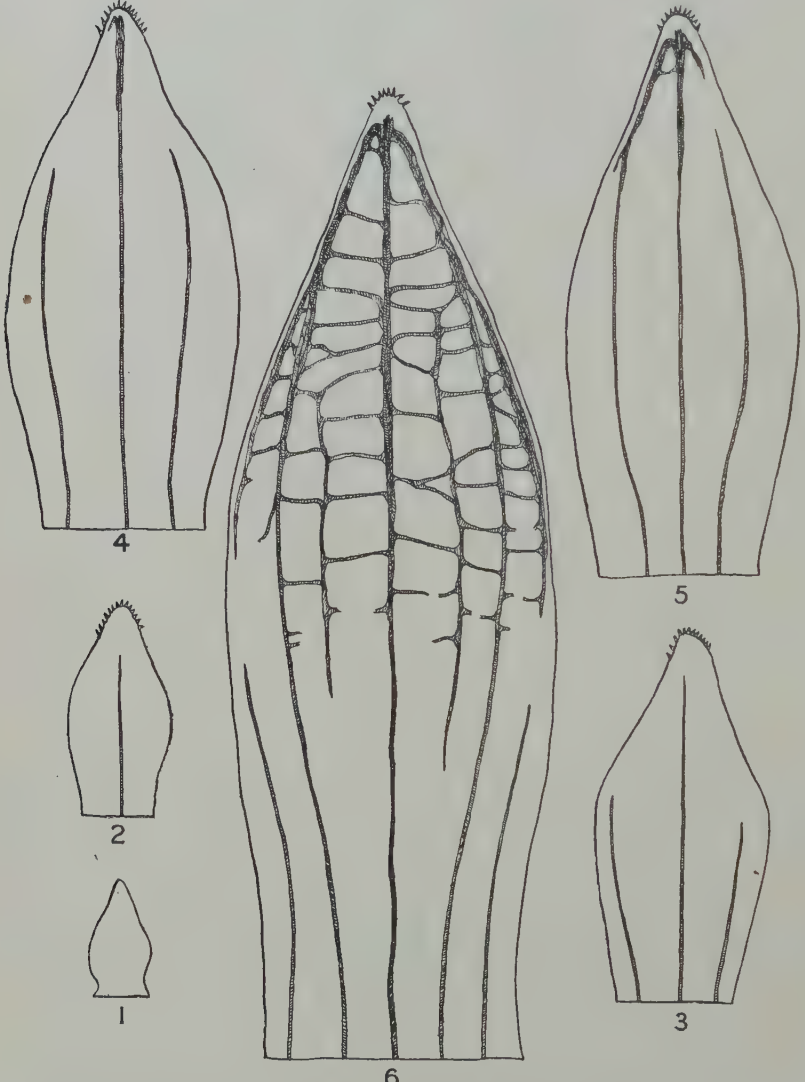


Diagram showing the course of the bundles in the stem.

length. The early differentiation of the protoxylem of the primary longitudinal veins in the lamina may be followed in a basifugal direction, but when the median vein reaches to within about four cells' distance of the leaf

FIG. 4.

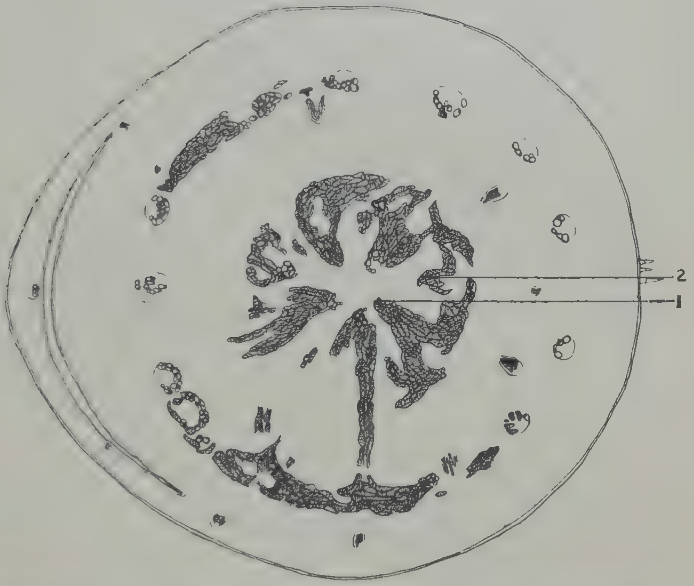


Series of leaves, showing stages in the development of the vein system in leaves with the following lamina length. (× 12.)

| | | |
|---|---|---|
| 1. 0·9 mm. | 3. 3·5 mm. | 5. 5·3 mm. |
| 2. 2·0 „ | 4. 5·0 „ | 6. 9·0 „ |

apex, it ceases to develop further in this direction, and tracheids are formed on either side of the end of the vein. From this terminal group of tracheids a vein begins to develop basipetally along each leaf margin, and as it passes down picks up the distal ends of the more lateral longitudinal veins. As the ends of these veins come in contact with the marginal ones, the tendency to basipetal development already at work in the latter causes the metaxylem of the lateral bundles to differentiate basipetally also. The general trend of differentiation back from the leaf apex is also shown by the first appearance in the apical regions of the leaf, of transverse veins, and also of secondary longitudinal veins, which arise from these transverse branches (fig. 4) (**3**, p. 148) (**20**). This type of leaf development, where the primary veins develop basifugally, entering the lamina when the latter is small and meristematic, whereas the secondary veins, both transverse and longitudinal, develop basipetally, is described by Prantl (**10**) as the usual type in Monocotyledons, and also by Schuster for Monocotyledons, and as occurring in various Dicotyledons with simple leaves (**20**). De Lanessan (**5**) describes a similar type in some detail for the leaf of *Artemisia Dracunculus*. In *Tradescantia* the basipetal vascular development extends throughout the leaf lamina and sheath as far as the leaf insertion. The secondary longitudinal bundles of the leaf then continue, and develop down the internode just interior to the peripheral ring as the cortical bundles of the stem. Some of these bundles persist the length of the internode, and

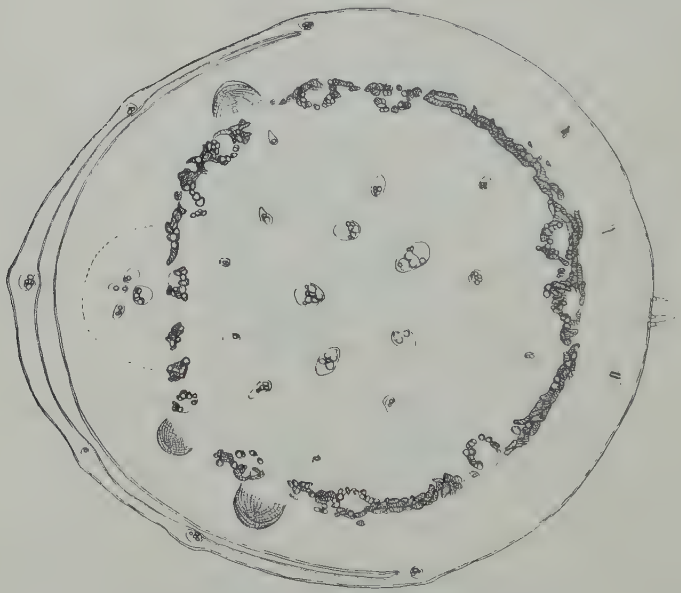
FIG. 5 *a*.



Transverse section through the nodal plate, showing the medullary bundles passing out to form the perimedullary bundles. (× 25.)
1. Position of medullary bundle.
2. " " new perimedullary bundle.

join on to the tissues of the node below, whilst others die out in the course of the internode (**8**, p. 66). The xylem-forming tendency passing down the primary longitudinal veins of the leaf cannot be carried down the perimedullary bundles, owing to the mature condition of the medullary tissues at this stage, and results in the formation of a ring of tracheids in the peripheral region of the node, where the tissues are less differentiated. From this nodal ring the peripheral bundles develop basipetally, as is clearly seen in longitudinal section, or by comparison of the state of differentiation of these bundles at the apex and base of elongating internodes (fig. 6). When fully formed, the peripheral bundles join on to the nodal ring of the node below, and anastomosing strands arise connecting the outer nodal ring and the central nodal plate (fig. 5 *a*). At the time the peripheral bundles are developing, the whole internode undergoes rapid elongation, the increase in length being brought about in the peripheral region by cell division and subsequent extension of the products of division, but in the medullary region almost entirely by the stretching of existing tissues, putting them under such strain that the rigid xylem of the medullary and perimedullary bundles is ruptured. Such disorganization of the xylem might be expected to have some influence upon the functional activity of these bundles, and experiments with eosin driven into the stem under slight pressure give results in accordance with this view.

Fig. 5 *b*.



**Transverse section through the outer nodal ring, showing the initials of the axillary bud and adventitious roots. (× 25.)**

### *Experiments with Eosin.*

Shoots of *Tradescantia*, with ends cut under water, were attached by rubber tubing to the short arm of a glass **U**-tube containing 1 per cent. aqueous eosin. The eosin was put under a pressure of 60 cm. of mercury, and left for two hours. Transverse sections of the mature internodes showed some eosin in the xylem cavities of the medullary and perimedullary bundles, but the staining was deeper and confined to the xylem vessels in the peripheral bundles, which obviously formed the only efficient conducting channels in this region of the stem. Buchholz (**3**, pp. 160, 163) lays considerable stress upon the importance of the xylem cavities as conducting channels in plants with intercalary growth, and especially in the Commelinaceæ, where the xylem of the medullary and perimedullary bundles becomes almost completely destroyed. The results of the present experiments with eosin are not, however, in accordance with this view. In the young internodes, the xylem of the medullary and perimedullary bundles was still intact and stained with the eosin, the peripheral bundles being as yet undifferentiated. In the elongating internodes a comparison of the number of stained xylem elements of the peripheral bundles at the top and base of the same internode also gave confirmatory evidence of the basipetal development of these bundles.

I. *Internode below the insertion of the 6th visible leaf.*

Xylem elements stained in the peripheral bundles.

| | *Top of internode.* | *Base of internode.* |
|---|---|---|
| Shoot 1......... | 12 | 9 |
| Shoot 2......... | 19 | 12 |

II. *Internode below insertion of the 5th visible leaf.*

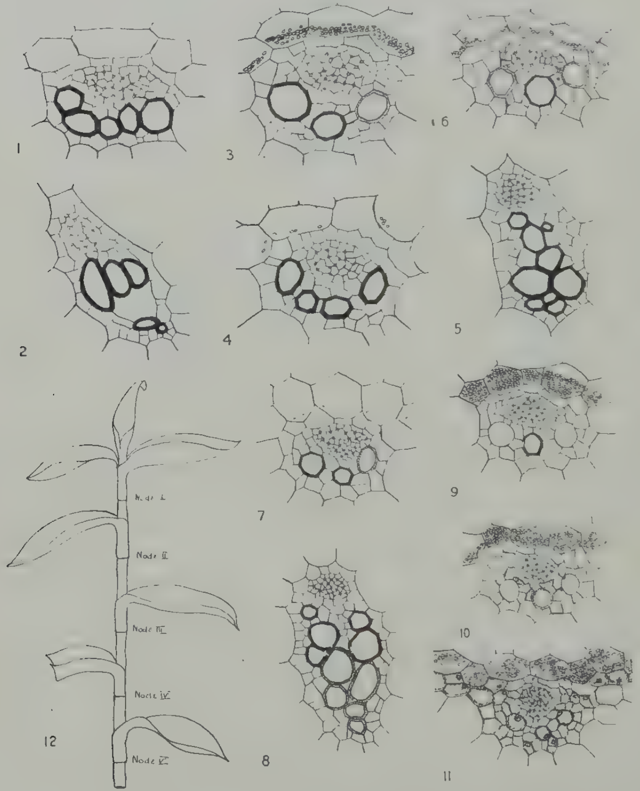
| | *Top of internode.* | *Base of internode.* |
|---|---|---|
| Shoot 1......... | 4 | 3 |
| Shoot 2......... | 11 | 4 |

When the peripheral bundles are differentiated through to the node below, the peripheral meristem ceases to divide as a continuous ring adding to the tissues of the internode (**3**, p. 141), but parts of it remain active and give rise to the axillary bud and adventitious roots. The vascular strands of the bud are derived partly from the nodal plate and partly from the outer nodal ring (**8**, p. 65), becoming arranged in the axis of the young branch, so as to reproduce the structure of the main shoot.

The initials of the adventitious roots form just above the insertion of the leaf and to the outside of the nodal ring (fig. 5 *b*), from which they eventually draw their vascular supply. Although the root initials may soon be distinguished in the young stem, they do not undergo further development until the leaf and usually the axillary branch of the same node are well developed. According to Wortmann (**25**), this formation of adventitious roots from the nodes is found in the majority of the genera of the

Commelinaceæ. An exception is found in the aerial stem of *Tradescantia virginica*, and this is probably due to the fact that the long leaves and internodes in this form are associated with long-continued activity of the basal meristem, and at the end of this period of growth the meristem is apparently no longer able to give rise to root initials. The underground stems with shorter internodes form roots in the normal way (**8**, p. 150).

FIG. 6.



Transverse sections of bundles to show differences in development at the base and top of internodes. (× 125.)

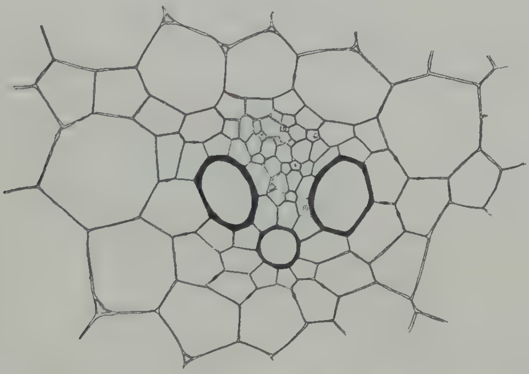
1. Below Node V. Peripheral bundle.
2. " " ". Medullary "
3. Above " " Peripheral "
4. Below Node IV. " "
5. " " " Medullary "
6. Above Node IV. Peripheral "
7. Below Node III. Peripheral bundle.
8. " " " Medullary "
9. Above " " Peripheral "
10. Above Node II. " "
11. Above Node I. " "
12. Shoot showing position of nodes in question.

## IV. HISTOLOGY.

The internodal meristem is localised in a peripheral position (**9**) and continues active longest at the base of the internode, as may be clearly shown by the chemical reactions of the cell walls and by the relative sizes of the cells at various distances up an elongating internode, this being especially easy to follow in *Tradescantia* owing to the very regular arrangement of the tissues in vertical series.

The cellulose reaction with iodine and sulphuric acid is given in fresh material by the parenchymatous tissues in older parts of the stem, and also, in the case of elongating internodes, by the tissues at the top of the internode and for varying distances down the medullary region according to the age of the internode. Chloriodide of zinc (Artschwager, **2**) gives no cellulose reaction on fresh material, but faint reactions are obtained after previous treatment of the sections with 5 % hydrochloric acid or Eau de Javelle, and heavy reactions after alcoholic potash. The most satisfactory results were given by some microtomed material, which had been fixed in chrom-acetic acid and taken up through the alcohols and chloroform to paraffin. Sections of this material reacted directly with chloriodide of zinc, all the parenchymatous tissues at the top of the internode giving a distinct blue colour, the latter extending much further down in the medullary region than in the peripheral, whilst the more basal and peripheral parts of the internode and the unlignified nodal tissues remained yellow. Tests for pectic substances in the middle lamella of differentiated cell walls with methylene blue or ruthenium red after previous treatment of the sections for one to several days in 25 % alcoholic hydrochloric acid or on microtomed material, embedded as already described, gave the same distribution as the cellulose tests, showing clearly that the peripheral tissues at the base of the internode and certain nodal tissues remain longest in an undifferentiated condition (**24**). As the cells pass out of the meristematic condition, they vacuolate and undergo considerable extension, so that the disappearance of the meristem may be clearly followed in a basipetal direction. As an example, the layer of cells lying immediately to the outside of the peripheral bundles may be considered in more detail. At the base of the internode the cells of this layer may be in a meristematic condition, showing in longitudinal section a

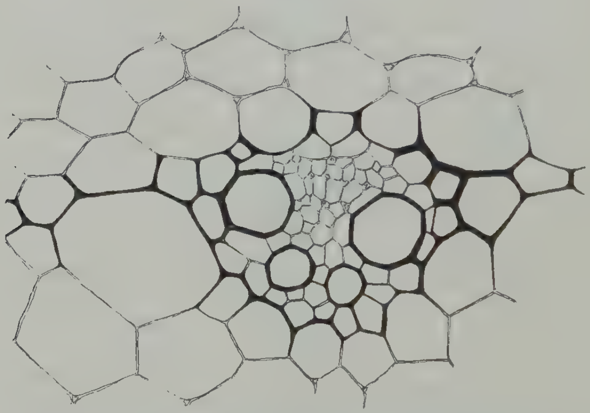
Fig. 7.



**Transverse section of a young peripheral bundle, showing the endodermis stage of the bundle sheath.** (× 235.)

greater width than height, e.g. $\frac{\text{Height}}{\text{Width}} = \frac{2}{5 \cdot 5}$. As the cells vacuolate, they stretch in a vertical direction, remaining of about the same width throughout the length of the internode, so that at the top of the internode the ratio may be $\frac{\text{Height}}{\text{Width}} = \frac{9 \cdot 0}{5 \cdot 0}$ or may be $\frac{4}{1}$ or more. As the cells elongate, starch grains appear in the cells of this layer, as in a typical starch sheath, but farther up the line of cells this starch disappears, and finally fatty substances are deposited on the walls of the cells, which ultimately form part of the sclerenchymatous sheath. All these stages may not be shown in the same internode, but may be traced through two consecutive internodes—one slightly extended and one almost mature. The other tissues of the internode show similar extension, but the cells maintain their parenchymatous nature. The parenchymatous tissues of the node also remain, potentially meristematic for a considerable time, and in these tissues arise the anastomosing strands which finally join the outer nodal ring to the inner nodal plate, and which probably develop when the tissues are irrigated by the peripheral bundles of the internode above.

FIG. 8.



Transverse section of a peripheral bundle, showing the sclerenchyma sheath. (× 215.)

The elongation of the internode does not take place until the vein system of the leaf is completed and the basipetal trend of differentiation is resulting in the development of the peripheral bundles, which apparently bring about the differentiation of the tissues of the peripheral internodal meristem as they advance. Consequently the cells of the layer immediately surrounding each peripheral bundle have at this time incompletely differentiated walls, and, owing to this fact and to their position between the bundle and the more mature surrounding tissues with air spaces, fatty substances diffusing out from the bundle are deposited on the radial walls in the form of a

Casparian strip (**13**, p. 123). The strip appears first on the walls of the cells opposite the phloem of the bundle, but finally forms a continuous primary endodermis round each peripheral bundle (**13**, p. 121 (fig. 7)). The Casparian strip shows at first as a small dot in transverse section on each radial wall, but, as a result of further diffusion of substances from the bundle and stretching of the wall, the deposit extends until it covers the entire radial wall and spreads to a less extent to the tangential walls and to some of the adjacent cells. Gravis (**8**, p. 29 and fig. 94) describes an endodermis in the hypocotyl of *Tradescantia virginica*, but does not record it as appearing in the course of development of the bundle sheath in aerial shoots.

About the same time, or slightly later, fatty deposits appear on the radial walls of some of the cells joining the peripheral bundles. These appear first either on the walls of the cells on either side of the bundle sheath or sometimes on the walls of cells about mid-way between the peripheral bundles, but finally are found in a complete ring of tissue, one or more cells in thickness, which encircles the medullary region of the stem forming the sclerenchyma sheath. The mature appearance of this sheath is similar to that of the bundle sheaths, from which it differs only in not being preceded in development by a primary endodermis stage. The unequal deposit of the fatty substances (fig. 8) on the different walls of any cell of the sheath make it evident that the fats become fixed here as they are diffusing along the walls, probably coming from the developing peripheral bundles or the disintegrating medullary and peripheral bundles and not from the sheath cells themselves (compare the formation of the secondary endodermis, **13**).

The Casparian strip and the sclerenchyma sheath give similar microchemical reactions, but the strip is more resistant to the action of strong sulphuric acid, by means of which the bundle endodermis may be separated from the other tissues as a cylindrical network with undulating walls. In both cases, the deposit gives the lignin reaction with phloroglucin and hydrochloric acid, and stains for fats with Sudan III in alcohol and glycerine. The fat appears to be acid in nature, giving the following reactions :—

Stains red with Methyl Red.
Stains greenish blue (Collenchyma bright blue) with Nile Blue.
Stains red with Dimethylamino-azobenzene, washed out with $\frac{1}{300}$ hydrochloric acid.

After treatment with 25 % alcoholic hydrochloric acid, the pectin reaction with methylene-blue is given by the sclerenchyma walls, but the middle lamella may still be distinguished as a darker line. Also, after treatment with alcoholic hydrochloric acid, the parenchymatous tissues macerate in 1 % ammonium oxalate or 10 % ammonia, but the sclerenchyma sheath remains intact.

By gently warming in strong potash, the fat may be removed from the layer of the wall of the sclerenchyma cells next the cell lumen, which then stains as an inner cellulose lamella with chloriodide of zinc, but the fat is not so easily removed from the rest of the wall. The formation of the sclerenchyma ring is affected by the exposure of the plant to light. Etiolation conditions have been shown to decrease the permeability of plant tissues (**12**, p. 38), and since in *Tradescantia* the formation of the sclerenchyma ring is dependent upon the diffusion of fatty substances along the walls, any changes in light conditions might be expected to affect its formation.

*Experiment.*—Well-grown plants of *Tradescantia* in pots were cut down to the level of the soil, and then grown exposed to electric light for definite periods each day:—

1. Continuous light.
2. 16 hours light per day.
3. 8 hours light per day.

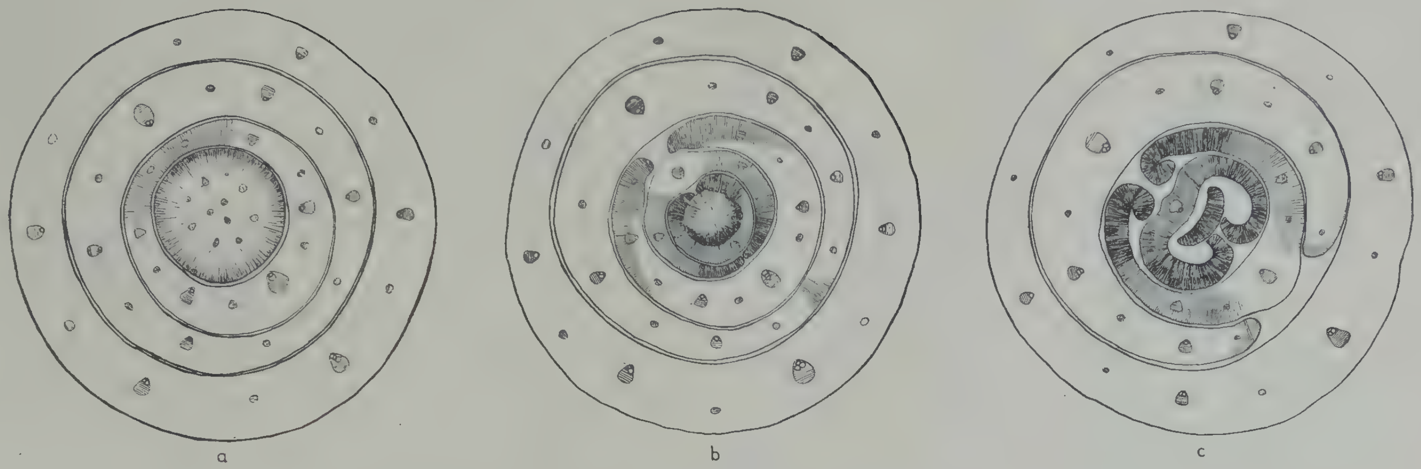
When the plants were well grown under these conditions, the development of the sclerenchyma ring was compared in the internode below the 8th visible leaf. These comparisons showed clearly that the development of the sclerenchyma depended upon the time of exposure to light, being well formed in continuous light and rather less so in 16 hours light, but showing only as a thin deposit in 8 hours light. In the extreme case of plants grown in darkness no sclerenchyma sheath is formed (**14**), but the Casparian strip of the bundle sheath forms as under normal conditions. Even in old internodes, the walls of the sclerenchyma are thicker at the top of the internode than at the base, where the stem is enclosed by the leaf sheath, and so protected from light.

## V. LEAF DEVELOPMENT AND REACTION TO ETIOLATION.

### *Origin of the Leaf.*

The mature leaf of *Tradescantia fluminensis* consists of a closed sheath, about 5 mm. in length, connected by a narrow portion to a lamina, which is usually about 60 mm. in length and 20–30 mm. in width. The leaf arises as a fold of tissue, which partly surrounds the stem at the base and narrows off above to a blunt point. Trécul (**22**) came to the conclusion that in Monocotyledons the sheath is the first part of the leaf to be formed, arising as a complete ring of tissue from which the lamina develops later. In *Tradescantia* it seems more appropriate to use the term applied by Eichler and quoted by Deinega (**6**, p. 444) of "leaf primordium" (Primordialblatt), and to regard this as differentiating later into sheath and lamina.

Fig. 9.



Transverse sections of shoot to show the distribution of unvacuolated tissue (shaded). (× 45.)

*a.* About 180 μ below stem apex.
*b.* „ 70 μ „ „ „
*c.* „ 80 μ above „ „

At this stage the leaf primordium and the region of the stem from which it arises are meristematic throughout, but cell-division is most active at the base of the leaf primordium and along its margins. The marginal growth of the basal part results in the two margins coming in contact and fusing to form the leaf sheath (fig. 9 *b*), whilst the growth of the upper parts leads to the formation of the broader lamina, the margins becoming rolled inwards (fig. 9 *c*). The different behaviour of the basal and upper parts may be due to the fact that the basal part is developing between the stem and the sheaths of older leaves, where the restricted space does not allow of the inrolling of the margin, whereas the upper part develops above the stem apex (fig. 9 *c*).

This origin of the leaf as a primordium in the form of an incomplete ring, which by subsequent growth forms a basal entire sheath and an upper lamina, agrees very closely with the formation of the leaf of *Dactylis glomerata* as described by Deinega (**6**, pp. 442–444).

### *Development.*

In the early stages of development, the growth of the lamina is rapid as compared with that of the sheath.

In the following table A, B, C, and D are different shoots of *Tradescantia*, and the measurements given are for sheath and lamina lengths of successive leaves :—

TABLE I.

| | *Sheath.* | *Lamina.* | | *Sheath.* | *Lamina.* |
|---|---|---|---|---|---|
| A. | 5·0 mm. | 30 mm. | C. | 4·8 mm. | 30·0 mm. |
| | 5·0 | 33 | | 4·5 | 25 |
| | 5·0 | 31 | | 4·3 | 22 |
| | 4·7 | 26 | | 1·2 | 18 |
| | 0·8 | 17 | | 0·6 | 9 |
| | 0·2 | 6·5 | | | |
| B. | 5·0 mm. | 31·0 mm. | D. | 4·0 mm. | 18·0 mm. |
| | 3·5 | 28 | | 5·0 | 21 |
| | 0·6 | 14 | | 3·8 | 20 |
| | 0·1 | 1·8 | | 0·3 | 12 |
| | | | | 0·1 | 2·2 |

As shown in A, the lamina has reached a length of 17 mm. (over half the length of a fully grown lamina of the same shoot) when the sheath is 0·8 mm. (about a sixth of the length of the fully grown sheath). But the next figures in A show a sudden elongation of the sheath, and the same point appears in the other sets of measurements.

Table II. shows the relative sheath and lamina lengths correlated with the stage of vascular development in the leaf :—

TABLE II.

| *Leaf.* | *Sheath length.* | *Lamina length.* | *Vascular development.* |
|---|---|---|---|
| *a* …… | 4·8 mm. | 31·5 mm. | Secondary longitudinal and transverse veins developed down to the sheath. |
| *b* …… | 5·0 | 28·0 | Secondary longitudinal and transverse veins developed down to the sheath. |
| *c* …… | 1·5 | 20·5 | Secondary longitudinal veins developed basipetally 16 mm. from leaf tip. |
| *d* …… | 0·4 | 7·0 | Basipetal development 2·5 mm. from leaf tip. |

Comparing the stages of leaf growth with vascular development, it is evident that the increase in length of the lamina takes place in all stages of leaf growth, but the elongation of the leaf sheath is slow until the basipetal vascular development in the lamina is sufficiently advanced to irrigate the tissues of the sheath, when a sudden extension of the cells takes place.

### *Differentiation of Leaf Tissues.*

The vacuolation of the leaf tissues follows the same course as the development of the vascular system, the cells beginning to differentiate rather ahead of the advancing veins. The method used for following the development of the veins was one used by Schuster (**20**). After removal of the chlorophyll by warming in methylated spirit, leaves were left to stand in a saturated solution of chloral hydrate until transparent—a time varying with the age of the leaf, from a few days up to about three weeks. The cleared leaves were mounted whole, in glycerine, when the xylem strands could be easily followed, especially after staining in dilute methylene-blue. In this way the relative vascular development and leaf size could be compared, typical results being as follows (fig. 4, p. 6) :—

Leaf 1. Lamina length, 0·9 mm.
No vein in lamina.

2. Lamina length, 2·0 mm.
Protoxylem of median vein developed basifugally, 1·5 mm. from base of lamina.

3. Lamina length, 3·5 mm.
Protoxylem of median vein 0·4 mm. from leaf apex, and first lateral primary longitudinal veins developed to within 1·75 mm. and 1·94 mm. of leaf apex.

4. Lamina length, 5·0 mm.
Median vein developed to within 0·3 mm. of leaf apex and marginal basipetal veins starting to develop. First lateral primary longitudinal veins, 1·5 mm. and 1·6 mm. from leaf apex.

5. Lamina length, 5·25 mm.
   Median vein 0·15 mm. from leaf apex and marginal veins starting downwards from its apical end. One lateral vein joined to one of the marginal, the second lateral vein developed basifugally to 1·2 mm. from the leaf apex and the second marginal vein basipetally 0·6 mm. One transverse vein near leaf apex.
6. Lamina length, 9·0 mm.
   Marginal veins basipetally developed 3·9 mm. from the leaf apex, and the secondary longitudinal veins starting from the transverse veins and extending from 2·8 mm. from the tip to 5·6 mm., and from 2·0 mm. to 6·3 mm. respectively. Numerous transverse veins.

Fig. 10.

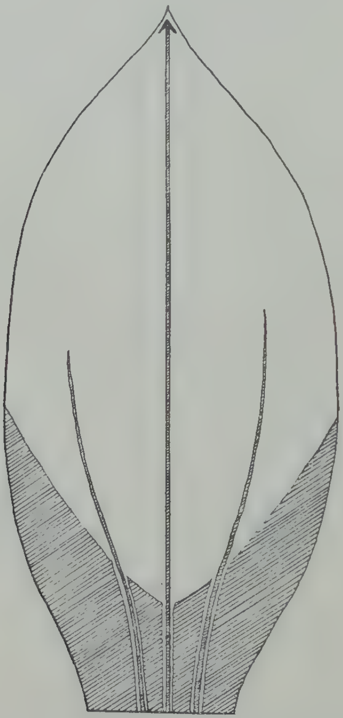


Diagram of a leaf to show the distribution of unvacuolated (shaded) cells of the upper epidermis. Lamina length 5·4 mm. (× 15.)

In the first basifugal development of the primary longitudinal veins, only the protoxylem is differentiated, and consequently this stage of vein formation has very little effect on the general differentiation of the tissues. For example, in a lamina 4 mm. long, the tissues are unvacuolated, except for a few cells in the immediate neighbourhood of the developing median bundle. (A similar case is also illustrated by Schüepp (**18**) for the young leaf of *Acer Pseudoplatanus* Linn.) The vacuolating effect of the developing bundles is most marked in the upper epidermis, which, lying next the xylem of the bundle, is the first part of the leaf to be affected, and vacuolation of this layer of cells extends for some distance round the bundle. Cells of the lower epidermis and mesophyll are also slightly vacuolated at this stage, but the closely fitting cells of the palisade tissue remain practically unaffected. When the median vein has reached the leaf apex and the direction of vascular development is reversed, all parts of the lamina gradually come to lie within the "sphere of influence" of the vein system and differentiation of all the tissues proceeds rapidly in a basipetal direction, but always advancing more quickly in the median than in the marginal parts of the lamina. This is shown in fig. 10, a diagram constructed from serial microtome sections across a leaf of 5·4 mm. lamina length, and showing the regions of unvacuolated (shaded) cells of the upper epidermis—vacuolation having proceeded farthest down the lamina round the median vein. It is clear from these facts that the basal and marginal regions of the lamina continue actively meristematic longer than the median parts and this continued activity leads to the formation of auricle-like extensions of the lamina beyond its point of insertion to the sheath (an effect more marked in leaves such as those of *Sagittaria*). When the vein system of the lamina is developed throughout the leaf, all the tissues of the latter are vacuolated and incapable of further growth. In plants of *Tradescantia fluminensis* exposed to bright light, the shoots are markedly dorsiventral and the leaves are asymmetrical about the median vein—the lamina being wider and the auricle most pronounced on the side most exposed to light.

### *Reaction to Etiolation.*

The development of the leaf in *Tradescantia* belongs to the type described by Sachs (**15**) (**12**), where the basal leaf meristem normally grows in the dark, surrounded by the bases of older leaves, and where the internodes remain short until the leaves are almost fully grown. Sachs finds that leaves of this type continue to grow in darkness, usually developing a longer narrower lamina than in the light. In *Tradescantia*, etiolated plants produce only very small weak shoots, with leaves that remain partially inrolled. In one case, an etiolated leaf was grown with a sheath 3·5 mm. long and a lamina 27 mm., but the majority of the leaves were considerably smaller. Apart from the small size, the chief point of interest was the narrow lamina in comparison to the length, as shown by the following ratios:—

$$\text{Normal green leaf } \frac{\text{Length}}{\text{Width}} = \frac{60}{28} \text{ mm.} = 2{\cdot}2.$$

$$\text{Etiolated leaf} \quad ,, \quad \frac{27}{8} = 3{\cdot}4.$$

$$\frac{21}{6} = 3{\cdot}5.$$

The etiolated leaves also differ from the normal in the absence of auricles, the laminæ tapering from the widest point, about halfway along the lamina to the sheath, and also in the symmetry of the lamina about the median vein.

Leaves from the undergrowth of the greenhouse gave results intermediate between those of etiolated and normal leaves with a

$$\frac{\text{Length}}{\text{Width}} \text{ ratio of } \frac{75}{28} \text{ mm.} = 2{\cdot}7.$$

In this case, the leaves were larger than the normal, but agreed with the etiolated type in the absence of auricles. Prantl (**12**, p. 37) showed, in the case of some leaf rudiments which fail to develop in the dark, that the meristematic cells are able to divide, but do not undergo the subsequent vacuolation and extension that normally take place in light. Considering the development of the leaf of *Tradescantia* under the various light conditions, in relation to Prantl's statement, a somewhat similar explanation may be suggested. The basal meristem normally develops in darkness, and consequently cell-division is unaffected, and continues under all three conditions, the differences in the size and shape of the lamina being due to the subsequent changes in the tissues, which normally take place on exposure to light. In the light, tissues emerging from the meristematic condition undergo vacuolation and certain changes resulting in increased permeability of intervening walls, thus allowing free access of sap to the meristem, whilst in darkness, although the tissues vacuolate, their walls remain relatively impermeable, impeding the flow of sap to the meristem and so limiting its activity. Consequently, etiolated leaves are smaller and narrower than the normal. The leaves in diffuse light have a normal or possibly extended period of meristematic activity and the light is sufficient to cause increased permeability of the tissues, with the result that the leaves are as large or larger than the normal, especially in length (if meristematic activity is long-continued).

The margins of young leaves are rolled inwards, the unrolling proceeding downwards, with general differentiation of the tissues. This unrolling is controlled by the extension of the palisade cells, and is unaffected by the differentiation of the upper epidermis, which takes place considerably earlier. The dependence of the unrolling of the leaf upon extension of the cells is also suggested by the fact that etiolated leaves remain permanently rolled, or only partly unroll very late in development.

## VI. DISCUSSION.

In this section it is proposed to recapitulate briefly the stages in the development of the foliar shoot of *Tradescantia*, with the view of ascertaining what light this specific study may throw upon the features characteristic of the Monocotyledon in general. Owing to our lack of knowledge of the factors controlling development, any interpretations of anatomical structure based upon development must, for the present, be only tentative in character.

### *Development at the Shoot Apex.*

In *Tradescantia*, and usually throughout the Monocotyledons, the essential features of the shoot are laid down by the primary meristem, which is, at first, restricted to the shoot apex. Portions of this primary meristem later become isolated and continue their activities as special meristems for the growth of the internode, leaf lamina, etc., but in no case do we find secondary meristems arising in vacuolated parenchymatous tissue. Consequently, when the primary meristem in the stems and leaves becomes vacuolated, no further growth of these regions of the plant is possible, except from isolated portions of the stem meristem, which remain undifferentiated as the initials of the axillary buds and adventitious roots.

It is obvious, then, that in any such plant, where secondary meristems do not arise, any interpretations of structure in terms of development must be based upon an understanding of the factors controlling growth at the shoot apex. Unfortunately these factors are, at present, very little understood, and any attempt to base the successive structural phases upon them must be quite inadequate. In *Tradescantia* the shoot apex consists of a blunt cone of tissue, surrounded by successive cylinders of leaf sheath. The superficial layers of this growing point consist of actively dividing cells, but this layer of meristem never reaches a greater thickness than 4–5 cells, behind which differentiation takes place very rapidly, making it possible to trace the procambial strands of the perimedullary bundles to within a few cells' length of the meristem. One of the essential features of the growing apex seems to depend upon the vertical distribution of the meristem cells. Across the top of the cone the vertical depth of the meristematic layer is 4–5 cells, whereas down the sides of the cone the depth may be considerably greater, and, owing to this greater number of dividing cells down the sides of the cone, a circular fold of tissue is thrown up above the apex as the primordium of the first leaf. The primordium does not grow up evenly round the apex, and actually separates as an interrupted ring, the position of the gap alternating in successive folds and corresponding to a rhythm in the development of the vascular strands.

This zonal upgrowth of leaf primordia at the shoot apex, and the relatively few leaf initials which clothe the apex at any one time, are characteristic of the Monocotyledon as compared with the Dicotyledon, which, in the same period of time, usually produces a larger number of smaller leaf initials, none of which are inserted by so wide a base on the shoot axis.

The result is that the larger leaves of the Monocotyledon are separated by longer plastochrones, in the sense that the term is used by Askenasy and Schüepp (**19**), and their insertion has a more profound effect upon the stem anatomy than in the case of the Dicotyledon. The Monocotyledon stem is, in fact, little more than an organ to carry the vascular supply for the season's leaf development, and, in the case of stems surviving for more than one season, serving to carry the vascular supply for the roughly equivalent leaf development of the following season. In this connection no further comparison of the leaf of the Monocotyledon and Dicotyledon as a morphological unit is attempted, such as that which is being developed on purely morphological grounds by Arber (**1**).

### *Vascular Development.*

It is a general phenomenon in *Tradescantia* that the development of the vascular strands always takes place in tissue which is just emerging from the meristematic condition, and that the impinging of a sap supply upon a region of active cell division appears to exert considerable influence upon it, tending first to accelerate cell division, which is then rapidly followed by vacuolation of the protoplast with consequent cessation of meristematic activity. In this way the procambial strands of vascular bundles appear close behind the shoot apex, and it is probably associated with the close proximity of these developing strands that the superficial meristem never reaches a greater thickness. Similarly, the vascular strands appear very early in the development of the leaf primordia, the second leaf fold behind the apex already showing strands entering the base of the vertical meristem, and so laying down the perimedullary bundles of the adult stem.

One conclusion from the developmental study of the stem bundles is that the perimedullary bundles from their first appearance are directed towards the base of the youngest leaf, and are essentially strands for foliar vascular supply from the start.

An important result of the vacuolating influence of a vascular supply upon meristematic tissue is seen in the way in which the perimedullary bundles bore their way out into the young leaf primordia, which are at first entirely meristematic and continuous with the apical shoot meristem. As the vascular supplies pass out into the leaf primordia this continuous layer of meristem is broken into a series of disconnected rings round the stem, each ring being separated from the next by a set of perimedullary bundles passing out into a leaf base. The most characteristic features of *Tradescantia* seem to result from the subsequent activities of these separated portions of the primary meristem, such as the lamina initial surmounting the leaf sheath and the intercalary zone of meristem. The activity of these latter zones leads to the extension of the internodes and causes the perimedullary bundles, instead of passing directly out into the leaf from the medullary position, to be carried up upon a "cauldron-shaped" mass of tissue for the length of one internode in an intermediate position (**21**). The result is, as both De Bary (**4**) and Suessenguth point out, that the leaf-trace in *Tradescantia* is actually inserted on to the leaf-trace of the next lower leaf, two internodes below the insertion of the leaf on the stem. It is therefore not unreasonable to regard the peripheral layers clothing the internode below the insertion of a leaf as foliar in nature. From the same developmental standpoint it is clear why the Commelinaceæ provide Saunders (**16**) with examples supporting "The Leaf Skin Theory of the Stem."

### *Leaf Development and the Foliar Vascular Supply.*

The origin of the leaf and the development of the vascular supply has already been traced in some detail, and it is only necessary to emphasise here certain salient features. The differentiation of the protoxylem of the median vein takes place basifugally, following closely upon the vacuolation of the meristem cells, but at the apex of the lamina the cells appear to vacuolate more rapidly, so that by the time the differentiation of the median bundle has reached to within a few cells' length of the leaf apex, it comes in contact with cells which are too mature to differentiate into xylem, and the vein is unable to develop further in this direction. The reason for the early vacuolation of the apical cells is uncertain, but may be connected with the greater exposure of these cells to the drying influence of air—a suggestion which is given slight support by the fact that apical hydathodes occur frequently in aquatic Monocotyledons such as *Zostera* spp. and *Potamogeton* spp. (**17**). In *Tradescantia* no apical hydathode is formed, and consequently a greater sap pressure is set up in the vein, which, acting on the younger cells on either side of it, causes them to give rise to a mass of short tracheids, from which the subsequent basipetal veins originate. This change in the direction of sap-flow, of which the appearance of the vascular bundles is an indication, is stressed again in this section of the paper, since it appears to be causally connected with some of the most characteristic features of *Tradescantia* anatomy and morphology. Owing to our lack of a wide knowledge of vascular development in the Monocotyledons, a discussion of the general significance of the basipetal development is not possible, but, since many of the resulting features are characteristic of the group as a whole, it is appropriate to point out the importance of this in such cases as it is known to occur. In the first place, in relation to our original problem, the backwardly directed flow of sap irrigates the basal meristem of the lamina, and is responsible for its long-continued activity, especially in the more marginal regions. A brief examination of the further possibilities of such a basal marginal meristem shows that it may have some bearing on leaf-shape. If the meristematic cells between the veins are sufficiently irrigated for a comparatively wide zone of cells to continue in active growth, the tendency will be for the veins to become more widely separated by intervening tissue. Such a condition as this, coupled with a long period of activity of the marginal wings of the basal lamina meristem, will tend to alter the shape of the leaf by the formation of basal auricles and to give rise to such leaf-forms as those of *Alisma*, *Arum*, and *Sagittaria*. On the other hand, if diffusion of sap proceeds with difficulty, there will be no tendency for the width of the meristem between the veins to increase, and, although the meristem may remain active for a long time, new cells will be added only at the irrigated surface, and so add to the length of the lamina. It has been shown in a previous study (12) that etiolation phenomena arise by the impeding of the flow of sap to the meristem-cells, and consequently the effect of etiolation conditions upon leaf development of the type shown in *Tradescantia fluminensis*, *Alisma*, etc., should be to produce longer linear leaves without the basal auricle. This is exactly the type of response that Glück (7) demonstrates in *Alisma* to conditions of darkness or submergence, and it has already been shown that etiolated leaves of *Tradescantia* differ from the normal in having an increased $\frac{\text{Length}}{\text{Width}}$ ratio.

In the second place, in vascular development, all the primary longitudinal veins showing basifugal development, with the exception of the median from the apex of which originate the marginal veins, become fused by their distal ends with the basipetally developing marginal veins. This gives rise to the closed system of venation, so characteristic of many Monocotyledons, and to the closely associated character of an entire leaf-margin, since no free vein-endings reach the margins to cause local outgrowths in the form of lobes, teeth, etc.

Thirdly, the bundles penetrate the basal meristem of the lamina and enter the leaf sheath. The cells of the sheath are peculiar in that they cease active cell division comparatively early in the development of the leaf, but then remain in a quiescent state and do not extend until irrigated by the later basipetal flow of sap, when a sudden elongation of the sheath takes place, accompanied by the appearance in it of subsidiary longitudinal veins and the addition of metaxylem to the primary veins. The basipetal differentiation of the leaf vein system through to the leaf insertion is followed by the appearance of the cortical stem-bundles and the outer ring of vascular tissue at the node, from which the peripheral bundles develop in a basipetal direction. The important physiological significance of this late basipetal development of the peripheral bundles consists in the fact that in this way new channels of supply are opened up, just when the older channels are being ruptured by the rapid elongation of the internode, but developmentally their origin may be traced back causally to the change in the direction of sap-flow initiated at the apex of the lamina. The basipetal development of the peripheral bundles is a striking feature of *Tradescantia*, which appears to have been missed in the earlier work. Gravis correctly describes these bundles, noticing their late appearance and acknowledging their right to be regarded as a separate system, but does not draw attention to their direction of development, and their importance as a second channel of communication after the rupture of the xylem of the medullary and perimedullary bundles. De Bary, in his text-figure, depicts the bundles as extending too far into the shoot-apex, with the result that he describes them as "cauline." In the strict sense that these bundles have no direct continuation into the leaf, they are cauline, but, from the developmental point of view, they are so closely connected with leaf development that the term "cauline" seems scarcely appropriate.

In describing the developmental sequence of the vascular system of *Tradescantia*, it has been necessary to make use of two assumptions, which require further experimental evidence before they can be regarded as reliable. It has been assumed that, for differentiation of new xylem to take place, it is necessary for a sap-pressure to be set up in the existing xylem, and that the cells which are to give rise to xylem should be young. That the production of new xylem may be related to the sap-pressure in existing xylem is a hypothesis tentatively raised by one of us (**11**) in a previous paper, and since that time various facts have been noted, and to some extent investigated, which support this view. For instance, in the hydathodes of *Tropæolum* and *Fuchsia*, the breaking through of the xylem at the surface, allowing of exudation, may be brought about earlier by placing the leaves under conditions reducing transpiration and consequently increasing sap-pressure.

Although neither this factor of sap-pressure in existing xylem nor that of the state of differentiation of surrounding cells can be regarded as proved, the general facts of the formation of primary and secondary xylem are obviously in accordance with both these points, and the second one especially goes far to explain the developmental sequence of the vascular tissue in *Tradescantia*, first in its basifugal and secondly in its basipetal direction.

Finally, in connection with a previous study of etiolation (**12**) it may be pointed out that the type of etiolation response met with in *Tradescantia* and many other Monocotyledons agrees with the general standpoint there advanced. In the Dicotyledon the key to development under etiolation conditions was found to be the difficulty with which the nutrient sap diffused along the walls to the dividing cells, with the result that at the growing point of the shoot with its numerous small lobes of superficial meristem foliar development was practically inhibited. In *Tradescantia*, if a shoot already partly grown in light be placed in darkness, a number of zones of meristem are present, alternating with zones of differentiated tissue—these latter zones simplifying the problems of nutrition, since sap can percolate freely along the walls to irrigate the meristem. Consequently, these original zones of meristem maintain their activity, giving rise to longer internodes and to a long lamina, but, as in the case of the Dicotyledon, the flow of sap to the apex is impeded and apparently no further separation of zones of meristem or formation of leaf initials takes place after the shoot has been placed in darkness.

## VII. SUMMARY.

1. The investigation was started in the hopes of throwing some light upon the problem of sap supply to the upper parts of leaves which grow by a basal meristem, but has been extended as a developmental study of the shoot.

2. The scattered bundles of the stem may be classified into four groups—(*a*) medullary, (*b*) perimedullary, (*c*) cortical, (*d*) peripheral. At the nodes the bundles of the different series are in connection.

3. The bundles run up one internode in the medullary position, then bend out and run up the second internode as the perimedullary bundles which constitute the leaf-trace. The differentiation of the protoxylem of the primary longitudinal veins of the leaf takes place basifugally, but when this differentiation reaches the leaf-apex, the direction of sap-flow is reversed, with the result that the secondary longitudinal and transverse veins develop basipetally in the leaf, and lead to the basipetal development of the cortical and peripheral stem-bundles.

4. The internode grows by an intercalary basal meristem—the disappearance of which may be traced in a basipetal direction by the gradation in cell size and the micro-chemical reactions of the cell-walls in an elongating internode. The peripheral bundles develop in the region of the peripheral meristem, and in the course of development become surrounded by an endodermis, which is later converted into a sclerenchymatous bundle-sheath, continuous with the sclerenchyma sheath running round the stem.

5. The leaf primordium consists of an incomplete ring of tissue which later differentiates into sheath and lamina. The differentiation of the leaf-tissues follows the same general plan as the vascular development, taking place chiefly in a basipetal direction.

The effect of etiolation is to produce relatively narrower leaves.

6. The following points are discussed as being of importance in the development of the shoot in *Tradescantia*, and as probably bearing upon the Monocotyledon in general:—

(*a*) The absence of secondary meristems and consequent importance of the portions of the primary meristem, isolated as intercalary stem and leaf meristems.

(*b*) The zonal upgrowth of a few leaves from intercalary rings of meristem.

(*c*) The reversal in the direction of sap-flow from the apex of the lamina with its effect upon the irrigation of the basal meristem of leaf and internode, the formation of leaf auricles, and finally in the development of the peripheral stem-bundles as alternative channels of vascular supply to younger parts of the shoot when the older channels are ruptured by elongation of the internode.

(*d*) The zonal distribution of meristem accounts for the continued growth of partly developed leaves under etiolation conditions. No new leaf initials separate from the apex during growth in darkness.

7. It is shown that the change in shape of the leaves of *Alisma*, when grown in darkness, might be anticipated from a consideration of the developmental conditions under which the expanded lamina is formed.

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# On the Occurrence and Distribution of *Festuca ovina* L., sensu ampliss., in Britain. By W. O. Howarth, M.Sc., F.L.S., Lecturer in Botany in the Unversity of Manchester.

(With 2 Text-figures.)

[Read 3rd April, 1924.]

## Introduction.

The various forms of *Festuca ovina* L. occurring in this country, as seen in the Herbaria at the British Museum (Natural History), Kew, and at Manchester, have been sorted out in the light of Hackel's Monograph (1882) on the European Festucas and carefully examined. The author has also collected, or had sent to him, specimens from different parts of the country. He has emended, as the result of these observations on fresh and dried material, the original descriptions of those responsible for the naming of the plants in question, together with those of Hackel (*l. c.*) and Ascherson and Graebner (1900), applying these descriptions to a collection of plants rather than to a type-specimen. He hopes that his efforts will result in a wider recognition of these forms by collectors generally, and would be glad of the assistance of such in respect of the study of their further distribution from the ecological standpoint.

### *Description of the Species.*

### Festuca ovina L., sensu ampliss.

Plant usually forming a compact turf, grey-green to moderately bright green. Radical and culm leaves all similar; sheaths split to the base, or lower third part entire and not furrowed; ligules short, bilobed; laminæ all more or less complicate, 1–3- rarely 5-costate, with sclerenchymatous strands usually forming a continuous layer below the lower epidermis (see, however, Sp. II. *F. ovina* L. sensu strict.); vascular bundles, 5–7(–9). Panicle compact, linear before and after anthesis, its branches erect and generally somewhat rough.

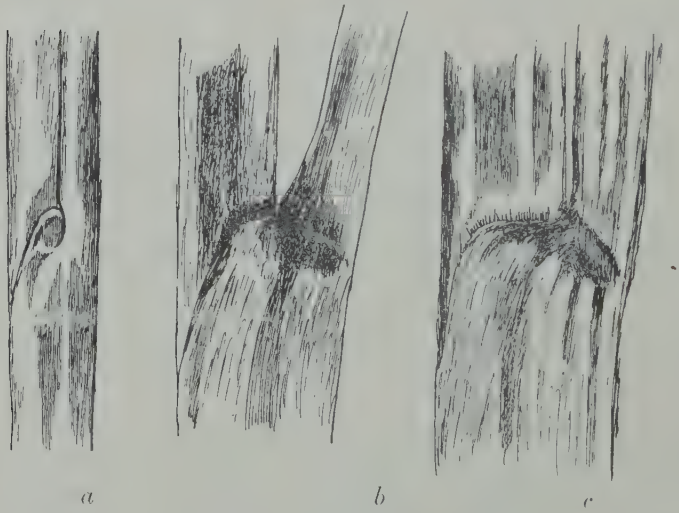
All our British forms belong to the subsp. *eu-ovina* Hack. (*l. c.* p. 85), distinguished largely by the bluntly pointed laminæ. They are his vars.:— 1. *capillata*, 2. *vulgaris*, 3. *supina*, 4. *duriuscula*, and 5. *glauca*. That named *duriuscula* by Hackel and others is not the one so named by Linnæus (Howarth, 1924, p. 325), and therefore this name cannot be allowed here, and has been replaced by the specific name *longifolia* Thuill. emend. mihi (Sp. IV., q.v.). Sp. II. *vulgaris* is the true *F. ovina* of Linnæus (1753, p. 73). All these forms are sufficiently distinct to be recognized as true species, and are so regarded by many authors. It is purposed to treat them as such here under I., *F. capillata* Lam.; II., *F. ovina* L.; III., *F. supina* Schur; IV., *F. longifolia* Thuill. emend.; and V., *F. glauca* Lam.

*Key to Species.*

1. Laminæ capillary or setaceous, 0·3–0·6 mm. diam., 5–7 vascular bundles.
    *a.* Fertile glumes not awned .......................................... *capillata.*
    *b.* Fertile glumes clearly awned.
        i. Radical sheaths entire only at extreme base .................... *ovina.*
        ii. Radical sheaths entire in lower third part, leaves rigid, with usually 7 v.b.'s.; culms low; panicle 2–4 cm. long .................... *supina.*
2. Laminæ sub-juncaceous or juncaceous, 0·7–1·0 or more mm. diam. (5–)7(–9) v.b.'s.
    *a.* Leaves green or glaucescent, not pruinose, rachis usually scabrous...... *longifolia.*
    *b.* Laminæ (at least at the base) and sheaths (at least above) and also to some extent the nodes of the culms pruinose; rachis smooth at the base or throughout its length .......................................... *glauca.*

Sp. I. F. CAPILLATA Lam. 1778, p. 597.
,, Nym. 1882, p. 829.
,, Richt. 1890, p. 93.
*F. eu-ovina*, var. *capillata* Hack. 1882, p. 85.
,, ,, ,, Aschers. & Graeb. 1900, p. 466.
*F. tenuifolia* Sibth. 1794, p. 44.

FIG. 1.



Ligules of radical leaves of *Festuca*.
(a) *capillata*; (b) *ovina*; (c) *supina*. All ×40.

Culm slender, to 40 cm. high, below the panicle angular or almost rounded, and scaberulous or almost smooth or puberulous: 2 nodes. Leaves with sheath open to the base, smooth or feebly rough, ligule auricles prominently lobed (fig. 1, *a*), and laminæ capillary or sub-setaceous (0·3–0·5 mm. diam.), rounded (almost circular) in transverse section (fig. 2, *a*), rough about the tips (or altogether in var. *hirtula*), usually longer than in Sp. II. following, bright green; usually 5, rarely 7, v.b.'s. Panicle erect, 2–8 cm. lg., compact and usually contracted so as to appear almost like a simple spike on account of its appressed, distant rachillæ. Rachillæ angles rough; spikelets small (3·0–5·5 mm. lg.), elliptical, compact, 3–8 flrs. Fertile glumes 2·5–3·7 mm. lg., lanceolate, acute, muticous or shortly mucronulate, smooth or with scaberulous apex, green, or golden- or brownish-green. Anthers 1·5–1·75 mm. long, yellow or violaceous.

Records from vice-counties 4, 9, 10, 11, 16, 17, 20, 21, 22, 35, 36, 38, 41, 49, 58, 63, 64, 65, 66, 67, 69.

Viviparous forms have been collected from 49, 64, 65, 66, 69.

Var. *hirtula*. Hackel describes (B. E. C. Report, 1913, p. 512) under his var. *capillata* a subvar. *hirtula*, which has all its glumes covered with minute appressed hairs, spikelets a little larger (6–7 mm. lg.), lower leaves with spreading minute hairs, upper ones glabrous. The specimen so described is from Coniston, v.c. 69; other similar ones are from v.c. 11. Another specimen from v.c. 4, which might conveniently be placed here, has its leaves scabrous and margins of glumes ciliate.

Sp. II. F. OVINA L. 1753, p. 73, sens. strict.
„ Nym. 1882, p. 829; 1890, p. 339.
„ Richt. 1890, p. 93.
*F. eu-ovina*, var. *vulgaris* Hack. *l. c.* p. 86.
„ „ „ Aschers. & Graeb. *l. c.* p. 467.

Culms slender or somewhat rigid, –60 or 70 cm. high: below the panicle usually rather angular, scabrous or puberulous, rarely smooth; 2 nodes. Sheaths of leaves rather rough or quite smooth, sometimes hairy, entire only at the extreme base, the rest open with edges overlapping; ligule auricles rounded (fig. 1, *b*); laminæ capillary or setaceous (0·3–0·65 mm. diam.), lax or somewhat firm, green or glaucous-green, not pruinose, usually scabrous, sometimes hairy, especially above ligule, in transverse section rather more keeled than the preceding; 5–7 v.b.'s, and sclerenchyma not so well developed in our British plants, forming a thin layer usually broken between the vascular bundles, and rarely almost absent (fig. 2, *b*). The glaucous-green forms are those which have a continuous layer of sclerenchyma, and often in addition a thicker cuticle. Panicle more open than the preceding, varying much in size, 2–12 cm. long, branches rough, obliquely ascending. Spikelets larger, 4·8–8·0 mm. lg., broader, 3–8 flrs., green or dark violet, pale green in the shade. Fertile glumes 3·4–5·0 mm. lg., lanceolate, mucronate or with distinct awn 1 mm. or more long.

The shape and structure of the transverse section of the radical laminæ and the form of the ligule auricles are quite useful criteria in determining this species, especially where dealing with viviparous forms. Hackel recognizes five subvarieties of his variety *vulgaris*, but only three of these appear to be present in this country :—

*α genuina*, *β hispidula*, *δ firmula*.

*α genuina* is the type and *β hispidula* is clearly distinguishable from it by its hispid glumes with ciliate margins. Whether it is ecologically distinct the author is not prepared to say at present. He has found a colony of it occupying an exposed heather moor above Taddington, Derbyshire, whereas the ordinary and the glaucous-green forms of *genuina* occur on the sides of the limestone dales below. Observations in other localities point to exposure rather than a difference in substratum as the deciding factor—*e.g.*, in the Lake District var. *genuina* is a constituent of the turf on the sheltered slopes, but var. *hispidula* is almost or quite pure in the scanty turf on the exposed mountain summits, especially where subject to wind erosion. *δ firmula* represents the larger, more robust phases of *genuina* found in the lower-lying districts on richer soils. Experiments now in hand seem to show that there is a tendency for *genuina* under cultivation to attain this larger state, and in a large number of forms examined one finds finer-leaved forms with the larger spikelets and glumes characteristic of *firmula*, and stouter-leaved forms with the smaller spikelets and glumes of *genuina*. It is doubtful whether *δ firmula* can be regarded as a true variety, and the description is therefore only given tentatively, and includes those forms which most nearly agree with Hackel. Ascherson and Graebner regard *hispidula* (under *sciaphila*) as a shade form of *genuina*, and *firmula* (under *Lemani*) they distinguish mainly by its larger spikelets and glumes.

Var. 1. GENUINA. See Hackel, *l. c.* p. 86.

*F. eu-ovina*, *vulgaris*, *genuina* Aschers. & Graeb. p. 468.

Culms slender ; laminæ mostly lax, capillary or sub-setaceous (0·3–0·4–0·5 mm. diam.), green or glaucous-green, scabrous or scaberulous or even hairy below, 5(–7) v.b.'s. Panicle somewhat compact, spreading at anthesis. Spikelets 4·8–6·0(–8·0) mm. lg.; fertile glumes 3·4–4·6 mm. lg., mostly smooth, but may be rough about the tip.

V.c.'s 3, 4, 6, 11, 14, 16, 17, 26, 31, 34, 36, 37, 38, 40, 41, 48, 49, 55, 57, 58, 59, 62, 64, 65, 67, 69, 70.

A distinct glaucous-green form occurs in v.c. 57.

Viviparous forms of the type have been collected from v.c.'s 49, 65, 67, 69, 70. Some are only partially viviparous, and in one specimen from Snowdon (v.c. 49) a small plant with a normal panicle is growing from the bulbil of a completely viviparous panicle.

Var. 2. HISPIDULA. See Hack. p. 87.
*F. ovina*, b. *hispidula* Richt. 1890, p. 93.
*F. eu-ovina*, *vulgaris*, 1. *genuina*, b. *sciaphila* Aschers. & Graeb. p. 468.

As var. 1, but the backs of the flowering glumes minutely hispid; margins ciliate.

V.c.'s 1, 11, 17, 29, 41, 42, 48, 49, 57, 59, 65, 69, 70, 71.

? Var. 3. FIRMULA. See Hack. p. 87.
Incl. *F. eu-ovina*, *vulgaris*, 2. *Lemani* Aschers. & Graeb. p. 468.
= *F. ovina*, d. *firmula* Richt. *l. c.* p. 93.

Culms somewhat rigid; sheaths smooth; laminæ setaceous (usual diam. 0·6 mm.), somewhat firm, scabrous or feebly so, green or subglaucescent; 7 v.b.'s, 2–4 layers in sclerenchymatous stratum, which is rarely interrupted. Panicle oblong, open at anthesis, somewhat dense, lowest branch less than one-third length of panicle. Spikelets large, 6·0–8·0 mm. lg.; fertile glumes 4–5 mm. lg., scabrous or hispidulous backs, towards the margins usually more or less ciliate, rarely glabrescent.

V.c.'s 23, 24, 57, 58, 69.

Sp. III. F. SUPINA Schur, 1866, p. 784.
„ Nym. *l. c.* p. 829.
„ Richt. *l. c.* p. 93.
*F. eu-ovina*, var. 3. *supina* Hack. *l. c.* p. 88.
„ „ *b.* „ Aschers. & Graeb. *l. c.* p. 468.

This species is recorded as occurring locally in the more mountainous districts of the British Isles, but in the several herbaria examined no specimen has been found preserved from any locality in Britain, and only one plant, the viviparous form, has been found from Scotland (v.c. 92). Plants collected in Europe have been examined, and Hackel's description emended from these.

Culm 12–30 cm. high, rigid, 2 nodes, four-angled below the panicle and scaberulous or puberulous. Leaf-sheath closed in the lower third or quarter, smooth; lamina 0·5–0·6 mm. diam. with a continuous layer of subepidermal sclerenchyma, 1-costate, elliptical in t.s. (fig. 2, *c*), not keeled, green to glaucous-green, rigid, setaceous and usually as long as or longer than the culm; 7(–5) v.b.'s; ligule only shortly auriculate, auricles ciliate (fig. 1, *c*). Panicle –4 cm. lg., compact, poor in spikelets, branches scaberulous or puberulous. Spikelets 6–8(–9·5) mm. lg., 4 flrs. Sterile glumes acuminate, upper 3-nerved at base; fertile glumes 4·0–7·0 mm. lg., smooth or hispid, with inconspicuous nerves, margins ciliate, green, violet, or dark violet, awn short.

Hackel places *F. ovina*, *vivipara* L. (1753, p. 73) = *F. vivipara* Sm. (1800, p. 114), as a subvariety of his variety *supina*. It apparently differs from the viviparous forms of *capillata*, *vulgaris* and *longifolia* in remaining constant under cultivation. The present author has not had the opportunity of testing this, but Linnæus, Withering, Smith, and Hackel agree. The specimen of *F. ovina*, *vivipara,* in the Linnean Herbarium agrees on the whole with *F. supina*, but those of Smith are clearly not all the same type.

Sp. IV. F. LONGIFOLIA Thuill. 1799, p. 50, emend. ; mihi.
*F. duriuscula* Pollich, 1776, p. 101.
*F. eu-ovina*, var. 4. *duriuscula* Hack. *l. c.* p. 89.
„ „ „ Aschers. & Graeb. *l. c.* p. 470.
*F. duriuscula* Nym. *l. c.* (*a*) 829 and (*b*) 339.
„ Richt. *l. c.* p. 94.

As has been shown in a previous paper (Howarth, 1924, p. 325) the plant named *F. duriuscula* by Linnæus is not a form of *F. ovina*, but of *F. rubra*. This name can therefore no longer be applied to the forms here described *.

Culm erect, rigid, 15–70 cm. high, 2 nodes. Leaves with sheaths closed only at the base, smooth or scaberulous or more or less pubescent ; laminæ setaceous, more or less rigid, 0·6–1·1 mm. diam., 3-costate, continuous layer of subepidermal sclerenchyma (fig. 2, *e*) green or glaucescent or glaucous-green, not pruinose, smooth, occasionally scabrous ; (5–)7(–9) v.b.'s. Panicle varied, 5–12 cm. lg. Spikelets elliptical or oblong-elliptical, 6–10 mm. lg., 4–9 flrs. Fertile glumes lanceolate, 4·0–5·5 mm. lg., awns –3 mm. lg.

## *Key to Varieties.*

1. Laminæ smooth or scarcely rough .................................... *genuina.*
2. Laminæ decidedly rough, especially about the tip .................... *trachyphylla.*

Var. 1. GENUINA.
*F. eu-ovina*, *duriuscula*, *genuina* Hack. *l. c.* p. 90.
„ „ b. „ Aschers & Graeb. *l. c.* p. 470.

Culm 25–40 cm. high, angular above, usually smooth. Sheaths glabrous, smooth ; ligule glabrous ; lamina 0·7–0·8–0·9 mm. diam., generally curved, smooth or only slightly rough along the infolded margins. Panicle short, 4–7–12 cm. lg., compact. Spikelets elliptical-oblong, 6–8–10 cm. lg. ; fertile glumes 4·5–5·5 mm. lg., smooth, shortly awned, awn 2 mm. lg.

V.c.'s 3, 15, 29, 36, 38, 39, 49.

Viviparous forms also in v.c. 49.

Forma *curvula*, leaves very rigid, scabrous ; v.c. 26.

Forma *longearistata*, awn more than half length of glume, glaucous-green ; v.c. 39.

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* The earliest name for one of the forms included in this group, *Festuca longifolia* Thuillier, 1799, is used in an emended sense to include all the forms, some with leaves not more than 2–3 cm. long.

Var. 2. TRACHYPHYLLA.

*F. eu-ovina, duriuscula, δ trachyphylla* Hack. *l. c.* p. 91.
„ „ „ Aschers. & Graeb. *l. c.* p. 471.
„ , „ Richt. *l. c.* p. 94.

Culm taller, 35–45 cm., more robust, scabrous above. Sheaths, especially below, shortly puberulous ; ligule feebly ciliolate ; laminæ subjuncaceous (0·7–0·8 mm. diam.) and scabrous on all sides, especially below the tip. Panicle 4–10 cm. lg., erect, compact, scabrous. Spikelets green to violet, 6–7 mm. lg. ; fertile glumes broadly lanceolate, 4–4·5 mm. lg., aristate, awn –3 mm. lg.

V.c.'s 15, 16.

Sp. V. F. GLAUCA.

*F. eu-ovina*, var. 6. *glauca* Hack. *l. c.* p. 94.
„ „ „ Aschers. & Graeb. *l. c.* p. 472.

Culm 20–40 cm. high, angular above (rarely rounded) and usually smooth ; 2 nodes. Leaves smooth, more or less pruinose ; sheath entire only at the base, ligule usually ciliolate, laminæ rigid, 0·7 mm. or more diam. ; 7(–9) v.b.'s, continuous sclerenchyma (fig. 2, *f* & *g*). Panicle –10 cm. lg., compact, rachis usually smooth or at least below. Spikelets 4–7 flrs., 5–6–8 mm. lg. ; fertile glumes lanceolate, 3·5–4 or 5 mm. lg., aristate or mucronate, more or less pruinose.

*Key to Varieties.*

1. Spikelets larger (7–8 mm. lg.), fertile glumes longer (–5·5 mm.) with longer awns (–2·8 mm.), rachis more or less straight ........................ *genuina.*
2. Spikelets smaller (6–7 mm. lg.), fertile glumes shorter (–4·7 mm.) with shorter awns (–1·5 mm.), rachis wavy ........................................ *cæsia.*

Var 1. GENUINA.

*F. glauca* Lam. 1789, p. 459.
„ Richt. *l. c.* p. 94.
*F. eu-ovina, glauca, genuina* Hack. *l. c.* p. 94.
„ „ „ Aschers. & Graeb. *l. c.* p. 472.

Culm 2–3 dm. high, somewhat robust, smooth above. Leaf diam. ·7 mm. or more (fig. 2, *f*). Panicle narrow, short, rigid, –5 cm. lg., axis straight. Spikelets 7–8 mm. lg., smooth, 4–5 flrs. ; fertile glumes 4·5–5·5 mm. lg., aristate, awn –2·8 mm. lg.

No county records except from cultivation.

Var. 2. CÆSIA.

*F. cæsia* Sm. 1808, t. 1917.
„ Nym. *l. c.* p. 829.
*F. glauca, cæsia* Richt. *l. c.* p. 95.
*F. eu-ovina, glauca, cæsia* Hack. *l. c.* p. 95.
„ „ „ Aschers. & Graeb. *l. c.* p. 473.

Culm smooth; leaves not less than one-half to one-third as long as the culm, 0·5–0·7 mm. diam. (fig. 2, *g*). Panicle 2–7 cm. lg., somewhat compact, axis wavy. Spikelets 6–7 mm. lg., 4–5 flrs.; fertile glumes linear-lanceolate, 4·2–4·7 mm. lg., smooth to somewhat rough, mucronulate-aristate, awn –1·5 mm. lg.

V.c.'s 6, 26, 34, 56.

Smith's plants gathered on the heaths round Bury St. Edmunds in 1804 are densely tufted with laminæ not more than 3 cm. long. Grown in Mr. Crowe's garden the leaves are 10 cm. long and about one-third the length of the culm. Much more recent plants from near Bristol (v.c. 34) have leaves half the length of the culm. Continental plants under this name are taller, have a larger, more open panicle (10 cm. long), but rather smaller spikelets and glumes.

## Discussion of Characters.

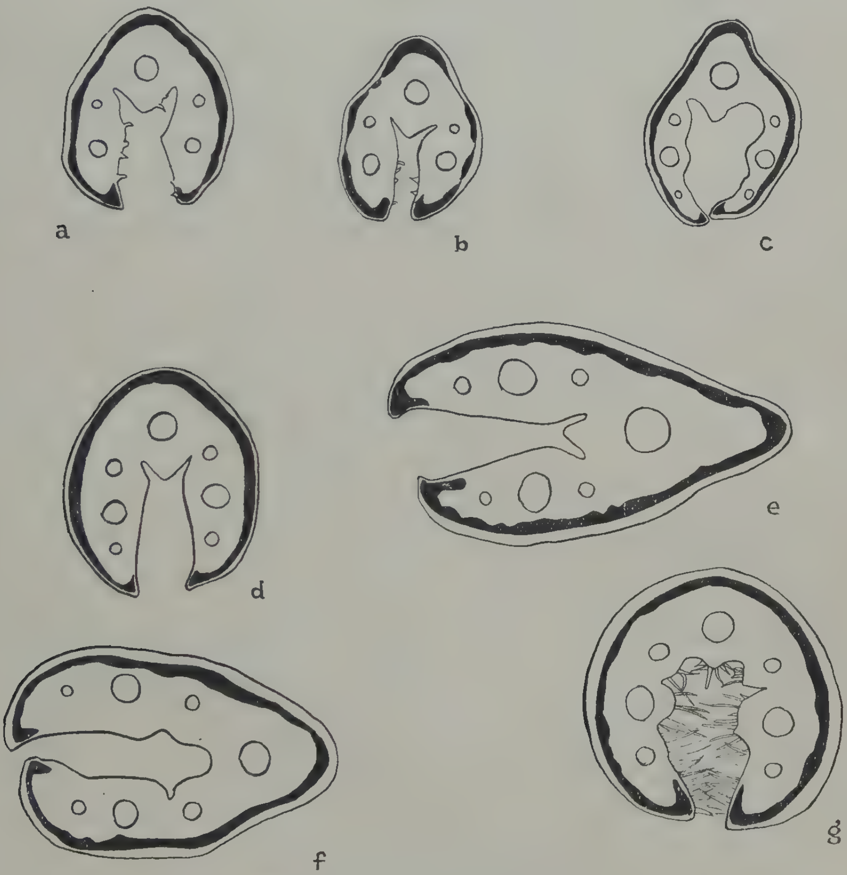
*Festuca ovina* can be readily distinguished from the cæspitose forms of *F. rubra* by the character of the branching at the base of the shoot. In all the forms of *F. ovina* intravaginal branches only are present, characterised by a dorsal, elongated prophyll followed immediately by the first vegetative leaf with normal sheath and lamina. In *F. rubra* forms the first branches of the shoots, if not all, are extravaginal, and these, even though they may be almost or quite erect, show a transitional series commencing with the minute dorsal prophyll through longer, sheathing scale-leaves to leaves with first a rudimentary, then a normal lamina (see Howarth, 1919, p. 270, fig. 2). Further, the open sheath of the radical leaf in *F. ovina* distinguishes this group from that of *F. rubra*, where the sheath is closed to its mouth. These characters are exceedingly useful in differentiating forms like *F. ovina, longifolia*, and *F. rubra, fallax*; *F. ovina, glauca*, and *F. rubra, pruinosa*.

For determination of the British forms of *F. ovina,* several characters have to be considered together. In *F. supina* and its variety *vivipara* reliance can be placed upon the sheath character, but in the absence of this the transverse section of the lamina is dependable along with the ligule. *F. glauca* and var. *cæsia* are pruinose—that is, have a definite waxy "bloom," which must, however, be carefully distinguished from the merely glaucous-green colour of other forms. *F. capillata* and *F. ovina, vulgaris* are finer-leaved forms distinguishable from *F. longifolia*. One finds that in all these forms the shape and structure of the lamina of the radical leaf as seen in transverse section is quite a useful and reliable character, though unfortunately in herbarium material it is not always available. For sectioning one chooses the next to the youngest leaf of any barren shoot and cuts the lamina at a distance of about a third its length above the ligule. In dried herbarium plants one cuts a segment of the leaf about a centimetre long from this region, places it for a short time in dilute alcohol in order to remove the air from the tissues, and then soaks in the following mixture (Orzeszko, 1903) :—

| | |
|---|---|
| Sodium carbonate | 5 gr. |
| Glycerine | 25 gr. |
| Water | 70 cc. |

This mixture can be slightly warmed if it is desired to hurry the process. As the leaf-segment is affected it changes colour gradually from the cut edges inwards, and when fully softened it can be hand-sectioned in pith. The histological characters of these sections can be observed as easily as in fresh material.

FIG. 2.



Sections of radical leaves of *Festuca.*

(a) *capillata* ; (b) *ovina* ; (c) *supina* ; (d) *supina, vivipara* ; (e) *longifolia* ; (f) *glauca* ; (g) *glauca, cæsia.* All × 90.

In all doubtful cases one turns, if possible, to the transverse section, and looks for further confirmation in the form of the ligule auricles (not in itself reliable); the smoothness, roughness, or hairiness of sheaths and laminæ; form of panicle; size and shape of fertile glumes; presence or absence of awns; and even, in the case of *F. capillata*, length of anthers. Even thus one finds that there are intermediate forms, especially between *F. capillata* and *F. ovina, vulgaris,* and to some extent between the latter and *F. longifolia* through var. *firmula.* In such cases it is necessary to sum up the characters in favour of the one or the other form, and place the plant on the side where the greatest weight of characters falls. This has been done, *e.g.* for the various agricultural races, otherwise they remain anomalous forms.

The viviparous forms of the various species, excluding *F. supina*, cannot in a few cases be determined with any degree of certainty. One is dependent mainly upon the vegetative characters of general habit, transverse section of lamina and form of ligule auricles, and often one or the other of these characters is in conflict with the rest. For the purpose of this paper, in the purely viviparous forms examined, reliance has in a few instances been placed entirely on the leaf-section. The author is not altogether satisfied with this, but, apart from observing these forms under cultivation, it is the only course open. But, although the leaf-section is fairly constant for any given species, it occasionally fails, even in normal-panicled forms, and it is reasonable to assume that the conditions which bring about those physiological changes seen in the transformation of a spikelet to a bulbil will also bring about changes in vegetative characters. Errors of determination cannot be excluded when dried viviparous forms are in question, and these may have to be revised should new facts be brought to light.

Vivipary in all the forms of *Festuca ovina* except *supina* may be induced, apparently by external environmental conditions existing at the time the panicle is being laid down. These conditions appear to be extreme humidity or drought. Thus it has been noted that vivipary is common during a wet season, or in plants growing in the wet peat of Eriophorum moor or under the influence of spray from waterfalls or rapid mountain streams, or, on the other hand, in rocky ground and dry soils generally. These observations, however, differ from those of Jenkin (1921, p. 418), who says he has never seen vivipary to occur in *Festuca ovina* plants which normally produce seed-bearing inflorescences. He suggests, though he has not investigated it systematically, that there is a distinct race of *F. ovina* of more than sub-varietal rank common to such situations as are enumerated above, in which vivipary is hereditary.

There is no doubt that *F. capillata* and *F. ovina, vulgaris* are indigenous to this country. Both are widely distributed, the latter more so than the former. Druce (1919, p. 847) says of *F. capillata,* "it is the plant of acid soils," and this in general seems to be true, but the statement that "*vulgaris* is the basic soil plant" is not confirmed by my observations that this plant is equally common on both siliceous and calcareous soils, although on the latter it forms a purer turf.

It is exceedingly doubtful whether *F. longifolia*, *F. glauca*, or its variety *F. cæsia* are indigenous, although the last was recognised by Sir J. E. Smith more than one hundred years ago around Bury St. Edmunds, and appears to have established itself on the banks of the R. Avon, Bristol, v.c. 34. Both *F. longifolia* and *F. glauca* are cultivated in Britain.

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# The Seedling Anatomy of some Species of *Lupinus*. By H. S. Holden, D.Sc., F.L.S., and A. Evelyn Chesters, B.Sc., University College, Nottingham.

(With 28 Text-figures.)

[Read 3rd April, 1924.]

The present investigation has been undertaken with a view to obtaining comparative data of the seedling anatomy of a number of species of the genus *Lupinus*. It was hoped that such a comparative study would yield some indication of the origin of the type of vascular structure characterising the various species, and, further, that the peculiarities known to occur in the juvenile anatomy of certain species would provide information as to the origin of what Dr. Miles Thomas has termed "diagonal symmetry" [12].

The species examined are seventeen in number and comprise the following: *Lupinus albus*, Linn., *L. angustifolius*, Linn., *L. arboreus*, Sims, *L. Barkeri*, Lindl., *L. Douglasii*, Agardh, *L. hirsutus*, Linn., *L. luteus*, Linn., *L. micranthus*, Dougl. *ex* Lindl., *L. microcarpus*, Sims, *L. mutabilis*, Sweet, *L. nanus*, Dougl. *ex* Benth., *L. nootkatensis*, Donn., *L. onustus*, S. Wats., *L. polyphyllus*, Lindl., *L. subcarnosus*, Hook., *L. sulphureus*, Douglas, and *L. varius*, Linn.

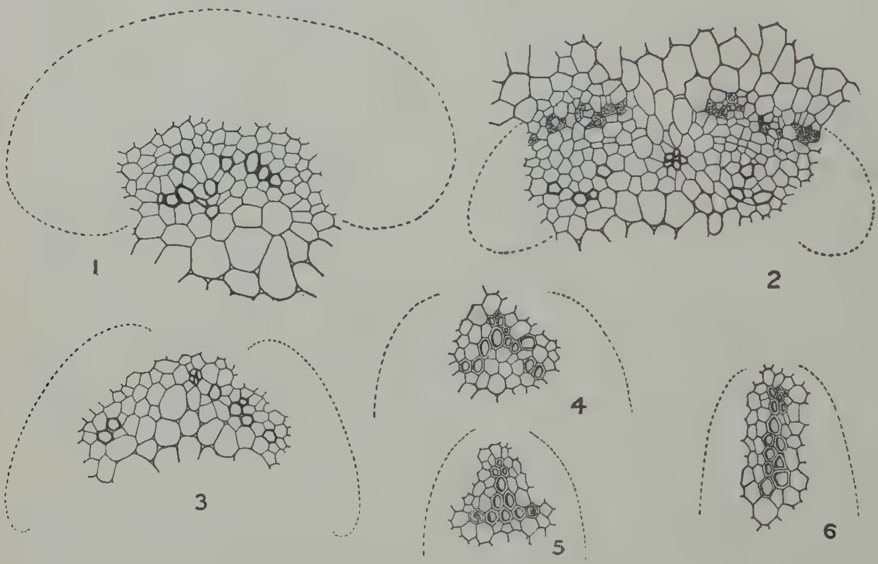
In view of the fact that the primary vascular structure is transient in the upper part of the seedling attention has been chiefly focussed on the young stages, although older seedlings have also been studied in connection with special points such as the behaviour of the epicotyledonary strands.

The seedlings are all of the same general type, the accumbency of the fleshy cotyledons giving them a characteristic lop-sided appearance. It is a point of some interest that, although in the majority of the species examined the contiguous faces of the cotyledons are relatively smooth, in three cases some degree of longitudinal ridging occurs. This is well marked in many specimens of *L. varius* and is strongly emphasised in *L. nanus* and *L. luteus*.

Anatomically the seedlings are characterised by a uniform diarchy, but, although this is the case, there is a considerable amount of variation in detail, two extreme types being recognisable. These are linked by a series of intermediate forms and appear to illustrate an evolutionary sequence. It is proposed to describe the transition phenomena in *L. nanus* first, as these approximate most closely to the condition found in the majority of diarch seedlings, and also as this species represents one extreme of the series.

The midrib, as in most of the species examined, is formed by two large strands which unite in the lower half of the cotyledon to form a collateral bundle (*cf.* fig. 1). This, at the base of the lamina, gives place to typical triad structure, the small central protoxylem being flanked by two well-developed phloem groups. On either side of the protoxylem, and frequently separated from it by one or two parenchymatous cells, a small group of metaxylem elements is situated. These appear to be developed in a tangential direction. The xylem elements arising subsequent to these develop centrifugally and, with the phloem, constitute two collateral groups in older seedlings. The condition described above is also found throughout the short petiole, but in the upper portion of the hypocotyl the metaxylem is represented by two tangentially elongated bands linked in the cotyledonary plane by the central protoxylem and forming with it a V-shaped group as seen in transverse section. At this level the laterally situated phloems have united with those of the second cotyledon to form two flanking plates. Towards the base of the hypocotyl the metaxylem forms a direct centripetal continuation of the protoxylem, giving rise to typical root-structure. Transition is thus, to use Compton's terminology, "intermediate-high" in type [3].

Figs. 1–6.



Transverse sections of part of the seedling vascular system of *Lupinus arboreus* at successively lower levels.

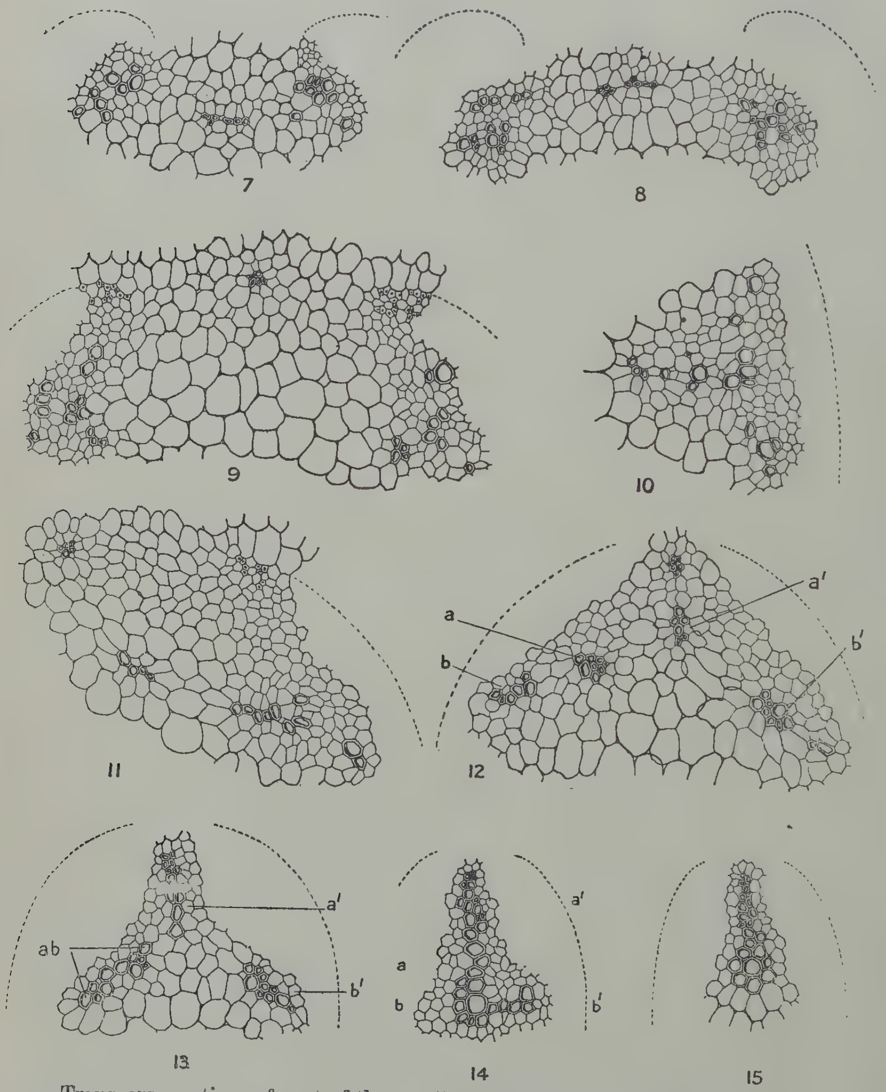
1. Cotyledonary midrib. 2. Petiole. 3. Middle of the hypocotyl—note the inequality in the development of the "vaisseaux intermédiares." 4. Base of the hypocotyl. 5. Just below the collet. 6. Root.

Comparing the transition characters in *L. nanus* with those of the ontogenetic scheme which Chauveaud [1] considers typical of diarch seedlings in general, it will be seen that there is a very close agreement. The primary metaxylem in the base of the hypocotyl is wholly centripetal in its development and is succeeded at a higher level by tangentially developed elements, these persisting even in the bases of the cotyledons.

The type of transition occurring in *L. albus* and *L. hirsutus* offers a sharp contrast to that occurring in *L. nanus*. As in that species the midrib develops triad structure near the base of the lamina, but instead of there being a close approximation between the central protoxylem and its flanking metaxylems, there is a gap of several (4–5) parenchymatous cells between them (fig. 7). In many cases tangentially developed metaxylem elements are absent, and the earliest metaxylem formed is associated with the lateral phloem groups, producing a pair of collateral bundles. One feature of considerable interest which frequently occurs in *L. albus*, and to a lesser extent in some of the other species (e.g., *L. hirsutus*), is the configuration of the protoxylem. In most dicotyledonous seedlings it forms a small compact group and frequently shows clear evidence of centripetal development, but in many seedlings of *L. albus* it takes the form of a transversely elongated bar, usually uniseriate though occasionally biseriate, which lies in a plane at right angles to the cotyledonary plane (figs. 7, 8). In some seedlings (fig. 8) the protoxylem may even be separated into two portions by an intervening parenchymatous cell. This type of protoxylem, although commonly found in this particular species, is not of constant occurrence, some seedlings exhibiting the more familiar compact central group of vessels.

Traced from the base of the cotyledons downwards there is a progressively wider separation between protoxylem and metaxylem, until, in the upper part of the hypocotyl, as many as twelve or fifteen cells of parenchyma may intervene between them (*cf.* fig. 9). The metaxylem groups, four in number, are thus situated immediately internal to the phloem groups in the diagonal planes. Their development at this level, as far as one can judge, is mainly or wholly centrifugal. While it is possible that the initial separation of protoxylem and metaxylem in the base of the cotyledon may be ascribed to the suppression in ontogeny of the tangentially developed elements, or, as Chauveaud [1] terms them, "vaisseaux intermédiares," an alternative explanation of the wider separation occurring subsequently will be made below. At a slightly lower level undoubtedly "intermediate" elements occur, and the protoxylem, in those cases in which it is transversely extended, contracts to the usual condition (figs. 9, 10). The number of "intermediate" elements increases at successively lower levels, but these invariably form a somewhat diffuse series, being grouped in twos and threes with parenchymatous elements separating them (fig. 10). In the region of the collet there is a tendency to greater continuity, but in many cases, as in the one figured (fig. 11), there is a definite separation into groups, one of which appears to lag behind in association with the centrifugally developed xylem elements. From this point downwards there is a slow approximation of metaxylem and protoxylem until typical root-structure is attained, usually 1·0–1·5 cm. below the collet. It is very common to find that the junction of protoxylem and metaxylem proceeds at a very unequal rate on the two sides. Thus in the example figured (figs. 12–15) the two groups of intermediate elements to

Figs. 7–15.



Transverse sections of part of the seedling vascular system of *Lupinus albus* at successively lower levels.

7. Top of the petiole. 8. Top of the hypocotyl. 9. Upper part of the hypocotyl. 10. Mid-hypocotyl, showing one metaxylem group only. 11. Collet. 12. Below the collet. 13–15. Root, showing the gradual development of root-structure.

the left of the protoxylem are labelled *a* and *b*, whilst those to the right are labelled *a′* and *b′*. Elements developed in continuity with those of *a′* first connect with the protoxylem. In the meantime, elements continuous with *a* and *b* have become united to form a single group which links up with the basal portion of *a′*, whilst those continuous with *b′* unite with the general mass last of all.

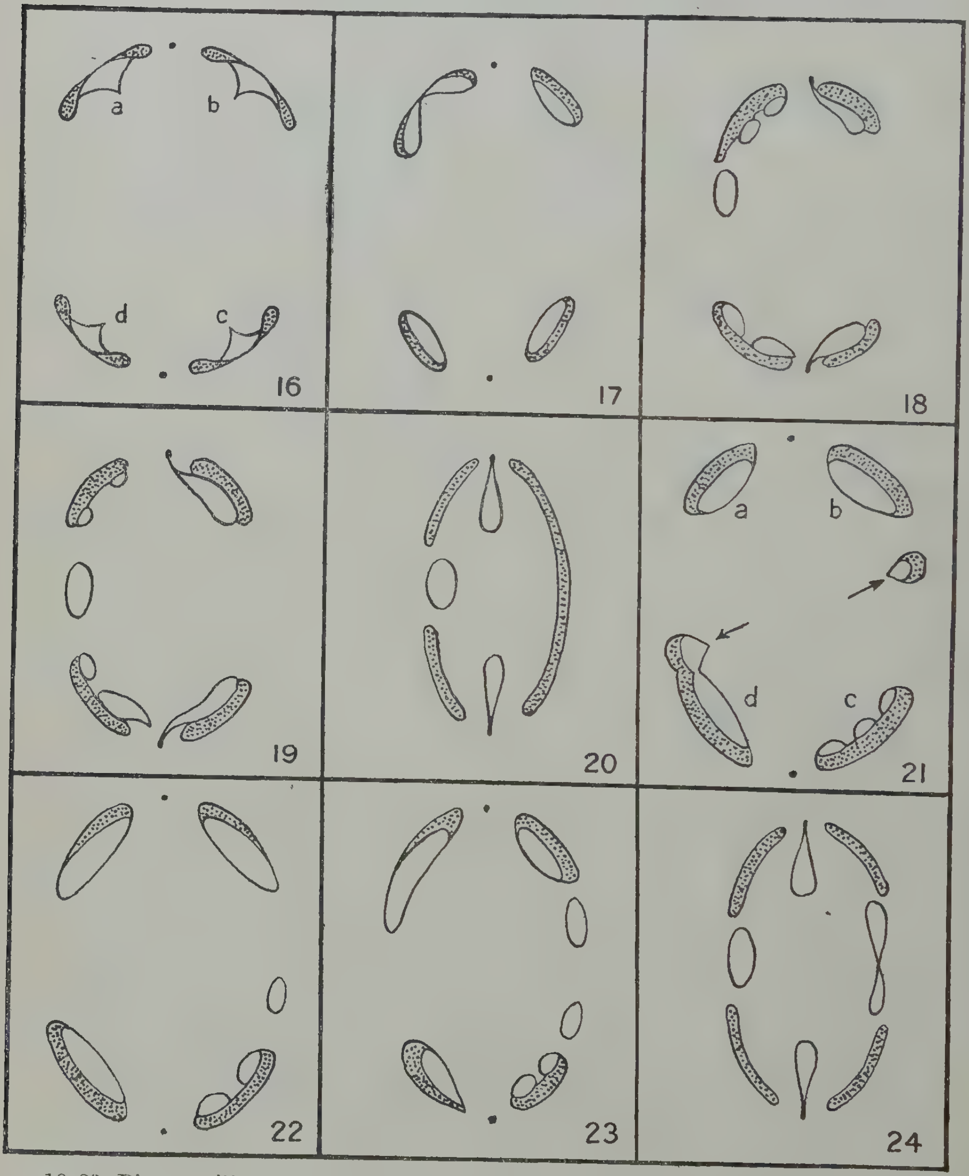
Comparing *L. albus* (and *L. hirsutus*) with *L. nanus* we see that the former differ from the latter in two important respects, namely, the wide separation of the protoxylem and the metaxylem in the hypocotyl, and the low level at which root-structure is attained. The transverse elongation of the protoxylem and the separation of the intermediate elements into two groups at the base of the hypocotyl, where they occur, also constitute further points of difference.

*L. nanus* and *L. albus* represent the two extremes of the series, and, anatomically, the remaining species may be arranged more or less in sequence between them.

Resembling *L. nanus* in type are *L. arboreus*, *L. micranthus*, *L. microcarpus*, *L. polyphyllus*, *L. subcarnosus*, and *L. sulphureus*. Of these, *L. microcarpus* and *L. sulphureus* resemble *L. nanus* most closely, whilst *L. arboreus* and *L. polyphyllus* depart from it most widely. All differ from it in two interesting respects, the first being in the tendency to show a parenchymatous gap between the protoxylem and metaxylem. This gap consists of from one to five cells: it may be absent, and is frequently more marked on one side of the protoxylem than on the other. Where the gap is lessened or eliminated the bundle is characterised by the development of "intermediate" elements, and these may be separated from the protoxylem, on the one hand, and the more distally situated metaxylem, on the other, by one or more thin-walled cells. The second point of difference between *L. nanus* and those species approaching it in vascular structure is the level of transition, which is always lower than that obtaining in *L. nanus* and is very generally completed at, or just below, the level of the external collet. The accompanying figures of the transition phenomena in *L. arboreus* will serve to illustrate these points. In figure 2 the condition of the cotyledonary strand as it traverses the petiole is shown. The separation between the protoxylem and the metaxylem there indicated is increased a little in the upper part of the hypocotyl, but a restoration of the "intermediate" elements begins in mid-hypocotyl (fig. 3), and near the base this restoration is completed so that a V-shaped xylem group results, whilst the phloems have united in the intercotyledonary plane to form continuous tangential plates (fig. 4). Immediately below the collet (fig. 5), the bulk of the metaxylem is centripetal, though a few "intermediate" elements persist, whilst a little lower down again these are not developed and typical root-structure is attained (fig. 6).

It will be noted that in the features in which the seedlings of the type described above tend to depart from the *L. nanus* type, they approach that of *L. albus*. In the remaining species examined the same tendencies are emphasised, so that the gap between protoxylem and metaxylem gets wider,

FIGS. 16–24.



16–20. Diagrams illustrating the transition in a pseudo-triarch specimen of *Lupinus varius*. 21–24. Diagrams illustrating the transition in a pseudo-tetrarch of *Lupinus varius*. The bundles indicated by arrows are of epicotyledonary origin.

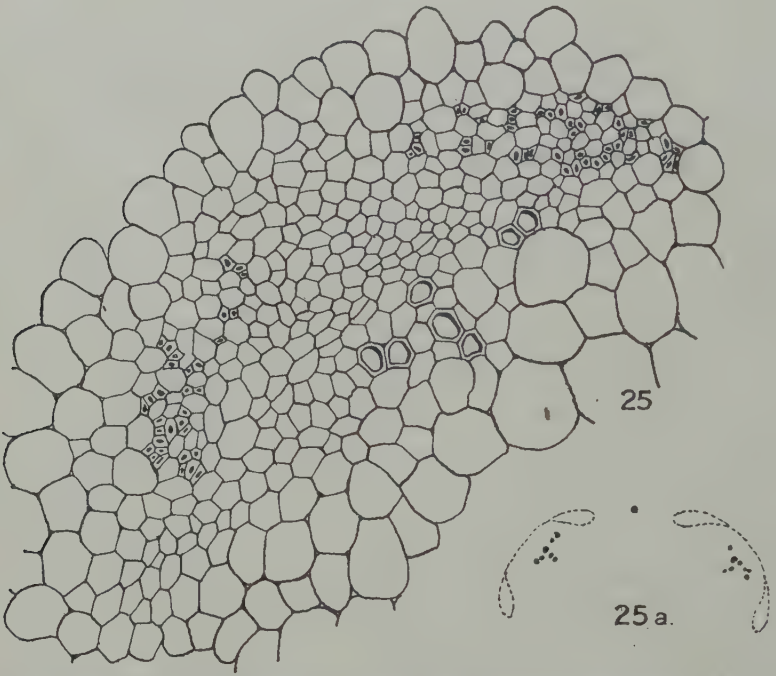
and the delay in the development of root-structure leads to the greater part of the transition occurring at and below the collet. The following list gives the maximum number of cells separating the protoxylem and metaxylem which have been noted in these remaining species :—

| Species. | Maximum number of cells. |
|---|---|
| *L. Barkeri* | 6 |
| *L. onustus* | 6 |
| *L. Douglasii* | 8 |
| *L. luteus* | 8 |
| *L. nootkatensis* | 8 |
| *L. angustifolius* | 9 |
| *L. mutabilis* | 9 |
| *L. varius* | 10 |

It will be apparent, from what has been stated above, that the whole of the species examined constitute, anatomically, a remarkably well-graded series with *L. nanus* at one end and *L. albus* at the other. Whilst there is no departure from the general plan in the majority of the seedlings studied, some few show variations which may be significant. The most important of these occur in *L. varius* and are concerned with irregularities in the behaviour of the xylem and of the phloem respectively. Those showing xylem irregularities are two in number. In the first of these the xylem structure of the upper part of the hypocotyl is quite normal (fig. 16), but at a lower level (fig. 17) the four metaxylem groups (*a*, *b*, *c*, *d*) take the form of tangentially elongated bands. Of these the two on the right of the protoxylems (*b* and *c*) gradually link up with these in the ordinary way (figs. 17–19). Of the others *a* divides into three parts and *d* into two (fig. 18). The adjacent portions of *a* and *d* unite in the intercotyledonary plane to form a xylem group which, though it does not develop a protoxylem, gives a pseudo-triarch appearance to the root (fig. 20), owing to the continued separation of the phloem groups. The proximal portion of *d* forms with *c* a root pole in the cotyledonary plane, but the two remaining portions of *a* dwindle and disappear, the second root pole thus being formed of half only of the metaxylem of the cotyledonary strand. The second seedling is broadly similar to that described above, but differs from it in detail. In this seedling two intercotyledonary xylem groups are formed in the root, so that a pseudo-tetrarch condition results. One of these arises from the union of the distal parts of the metaxylem groups *b* and *c* (figs. 21–24). The other is the product of the metaxylem group *a* alone which moves as a whole into the intercotyledonary plane. Metaxylem group *d* shows no abnormality in transition.

The first of the seedlings described above shares with several other seedlings, which are otherwise normal, a peculiarity in the behaviour of the phloem. This, as the bundles traverse the petioles, forms the usual cap to each of the four diagonally situated xylem groups. In the hypocotyl, however, each of the phloem groups divides into two, so that each metaxylem has associated with it a pair of phloem groups (figs. 25, 25 *a*). These are later reunited and behave quite normally in transition. A similar peculiarity in the behaviour of the phloem is occasionally met with in *L. hirsutus*. The remaining seedling showing abnormality is one of *L. luteus*, in which the bulk of the pith has died and shrunk for about half a centimetre. The cause of this is unknown, but a similar result may be produced by compression between finger and thumb. Whatever the cause of the injury in this particular case, a very vigorous reaction has followed. The whole of the living parenchymatous cells surrounding the wound, both intrastelar and cortical, have undergone elongation and division, producing fan-shaped masses of cambiform tissue which extend out into the space formed by the collapse of the dead pith cells (fig. 26). The secondary activity is not confined to the parenchyma immediately adjacent to the injury, but also includes that lying between the xylem and the phloem. It is interesting to note that a number of the cells derived from the division of the intrastelar parenchyma become lignified, forming tracheids, the thickenings of which are usually of the reticulate or spiral-reticulate type. They are, however, quite short, and show some superficial resemblance to the medullary tracheids of *Lepidodendron selaginoides*.

FIGS. 25 & 25 *a*.

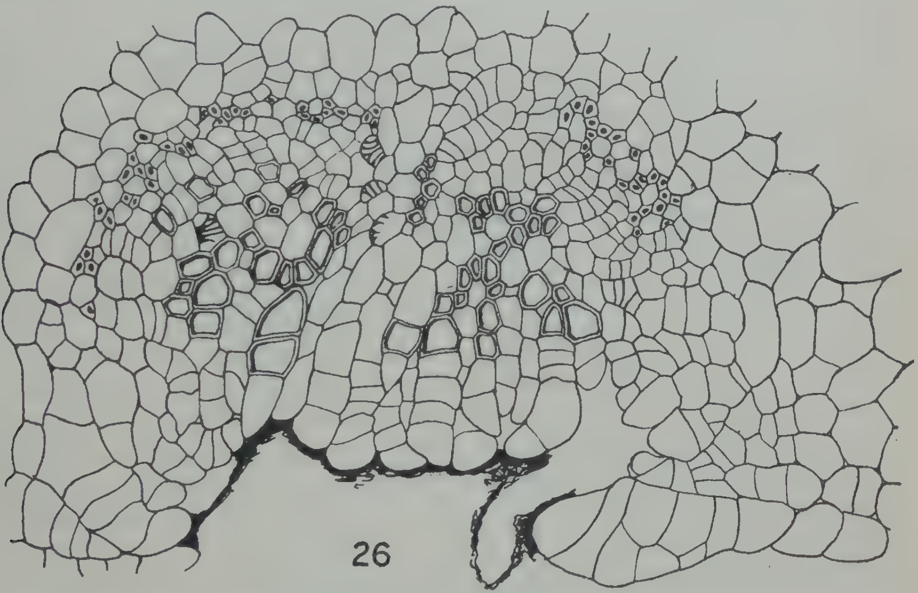


25. Transverse section of a diagonally situated bundle in the upper part of the hypocotyl of *Lupinus varius*, showing the bifurcation of the phloem. 25 *a*. Diagram showing the distribution of the vascular tissues in half the seedling.

The new cells resulting from the division of the cortical parenchyma do not, however, give rise to tracheid-like elements. Whilst the authors do not attach much importance to this difference, it has a certain interest in view of current theories as to the origin of the pith in Angiosperms. Wound-reactions of a somewhat similar character have been described by Dauphiné [**5**] in a species of *Lupinus* studied by him, in which they had been induced by the removal of the root-tip.

It may be noted in passing that Kattein's description [**10**] of the transition phenomena in *Lupinus luteus*, as Compton [**3**] suspected, is quite erroneous, these following the general lines shown by the other species examined.

Fig. 26.



26. Transverse section of a portion of the vascular system in a wounded specimen of *Lupinus luteus*, showing an extensive wound-reaction.

## Discussion.

Whilst it is evident that the seedlings examined may, from an anatomical standpoint, be arranged in a continuous series, it remains to be decided which of the two extremes represents the more primitive condition. The configuration of the vascular system in *L. nanus* is one which is characteristic of the great majority of seedlings exhibiting diarch symmetry, and, whilst this is not in any sense conclusive, there seems to be a considerable body of evidence from various published accounts of seedling anatomy, notably that of Miss Davey [**7**] on the Amentiferæ, that the lateral concentration of the metaxylem, and the consequent isolation of the central protoxylem, is a derived feature—a view to which we incline.

As was stated earlier, the initial stages in the disassociation of metaxylem and protoxylem may be readily explained by the assumption that the "intermediate" elements have ceased to be differentiated, and have been replaced by parenchyma. This view receives considerable support from the fact, to which reference has already been made, that the gap may be partly or wholly obliterated locally by the development of such elements. The inequalities in their development on the two sides of the protoxylem during their restoration at lower levels points in the same direction *. When the divergence between the protoxylem and its associated metaxylems becomes wider, spreading to eight, ten, or even fifteen cells, the mere elimination of the tangentially developed elements does not seem to provide an adequate explanation. The simplest one, and one which seems to fit the facts quite well, is that there has been a lateral movement of the metaxylem groups in phylogeny. Such an explanation receives support both from the behaviour of the protoxylem, which often becomes flattened or drawn out in a plane at right angles to the cotyledonary plane, and also from the straggling and disconnected character of the "intermediate" elements, especially in the upper half of the hypocotyl. A somewhat similar straggling is often shown by the "intermediate" elements occurring in the diagonal bundles of *Calycanthus*, and indeed the relatively simple type of diagonal symmetry exhibited by this genus would appear to have originated in a form showing diarch symmetry of the same type as *Lupinus albus*. As Dr. Miles Thomas [**12**] has shown, *Calycanthus* may exceptionally revert to the ordinary cruciform diarchy, and its resemblance to *Lupinus albus* must then be quite close. A further point in which certain species of *Lupinus* approach *Calycanthus* is in the precocious development of a small secondary collateral bundle between the widely divergent metaxylem groups. There is only one such bundle in *Lupinus*, however, and its appearance is much later than that of the series of such bundles characterising *Calycanthus*. In this connection the transition phenomena occurring in *Alnus cordifolia* [**7**] are also of interest, this species showing a diarch condition at the upper end of the hypocotyl and diagonal tetrarchy at the base, whilst in the intermediate region the two types of symmetry overlap. It may be that the transient bifurcation of each phloem group, which occurs in some specimens of *Lupinus varius*, has some significance in relation to diagonal symmetry, but it seems to show a definite divergence from the behaviour of the phloem in *Calycanthus* and *Alnus cordifolia*, since in both of these, as far as can be judged, the whole of the cotyledonary phloems move into the intercotyledonary planes, and that developing on the site of the cotyledonary protoxylem arises *de novo*. It should be noted, however, that Miss Smith [**11**] has described a permanent bifurcation of the phloem in *Payena Leerii*, one of the Sapotaceæ showing diagonal tetrarchy, which closely resembles the temporary condition characterising *Lupinus varius*.

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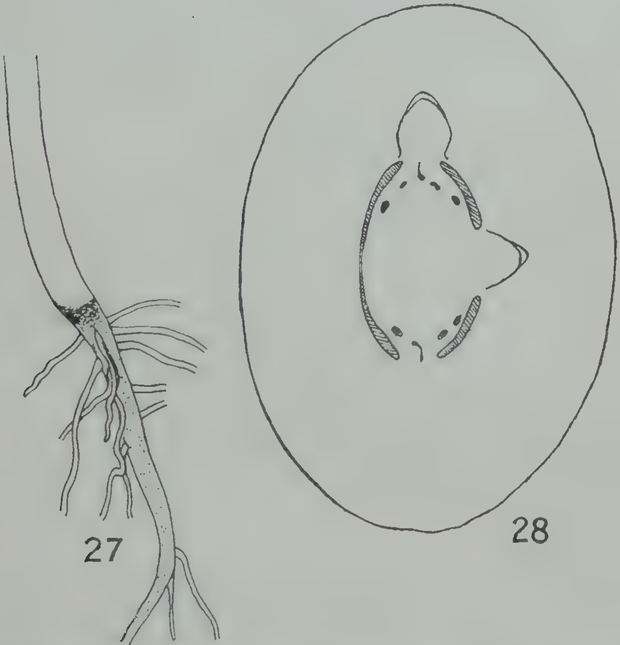
* M. Chauveaud has also called attention to this point in correspondence with one of us (H. S. H.).

In addition to the enquiry into the possible derivation of diagonal tetrarchy, the question of the source of the diarchy, which occurs throughout the genus *Lupinus*, may also be raised. Professor Compton, who, in 1912, submitted to this Society the results of a comprehensive investigation of the seedling-structure of the Leguminosæ [**3**], came to the conclusion that tetrarchy was the primitive type of vascular symmetry within the Order, and that diarchy, where present, was due to a reduction from a tetrarch condition. Though we are not prepared to subscribe without qualification to the view which regards diarch symmetry as necessarily reduced from a more complex type, such evidence as we have obtained lends support to Compton's contention. The evidence is yielded by the aberrant specimens of *Lupinus varius*, and also by others of *L. albus* and *L. hirsutus*. In the first of these the behaviour of the metaxylem during transition is the point of interest, part of this on either one or both flanks of the protoxylem becoming concentrated in the intercotyledonary plane, thus suggesting a partially successful attempt at

Figs. 27 & 28.



27. Part of the root-system of *Lupinus albus*, showing the lateral roots in four rows.

28. Transverse section of the root of a younger seedling of *Lupinus albus*, showing the origin of a cotyledonary and an intercotyledonary root.

the restoration of tetrarchy, even though no protoxylem is developed in connection with these groups. In *L. albus* and *L. hirsutus* it seems to us that the frequent division into two of the metaxylem during transition, and the tendency of the more distal part to lag behind, are further vestiges of an ancestral tetrarchy, and may be regarded as a subsequent stage in reduction to that shown by *L. varius*, where a pseudo-tetrarch condition obtains. Both these species, moreover, show an additional feature of some interest. It is a matter of common knowledge that the lateral roots generally arise in the plane of the root-poles of the tap-root, so that *L. albus* and *L. hirsutus* should bear their lateral roots in two ranks. As a matter of fact, in many specimens the lateral roots are borne in *four* rows, two in the cotyledonary and two in the intercotyledonary plane (figs. 27, 28). It seems reasonable to regard this as a survival from an ancestral tetrarch condition, necessitated perhaps by the relatively large size of the seedling in these two species.

## SUMMARY.

1. The seedlings of the seventeen species of *Lupinus* examined are uniformly diarch in plan.

2. They may, from an anatomical standpoint, be arranged in a series, with *L. nanus* at one end and *L. albus* at the other.

3. Commencing with *L. nanus* this series shows a progressively wider separation of the two metaxylem groups from the central protoxylem and a lowering of the level at which typical root-structure is attained.

4. It is considered that the initial stages in the separation of the xylem groups are brought about by the replacement of the tangentially developed elements termed by Chauveaud "vaisseaux intermédiaires" by parenchyma. This process is carried further, owing to a phylogenetic shifting outwards of the metaxylem groups.

5. It is considered that the final term in this series may represent one of the steps by which diagonal tetrarchy has been attained.

6. The evidence yielded by aberrant specimens of some species and commonly occurring variants of others is held to support Compton's view of the primitiveness of tetrarchy within the Leguminosæ.

The authors desire to record their thanks to the Regius Keeper of the Royal Botanic Gardens, Edinburgh, the Director of the Royal Gardens, Kew, the Director of the Botanic Gardens, Cambridge, and the Director of the Imperial Institute, London, for gifts of seeds, without which this work would not have been possible.

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# Phytoplankton of the English Lakes.

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## Introduction.

The English Lakes lie among the high hills of Cumberland, Westmoreland, and North Lancashire. These hills consist essentially of a central uplift from which run out ridges, radiating like the spokes of a wheel, and gradually decreasing in height as they pass further away from the centre. Practically all the main valleys between these ridges contain one or more lakes, varying greatly in size, but otherwise similar in appearance and characteristics. It is with eleven of the larger lakes that the present paper deals; Thirlmere, now practically a reservoir with variable water-level, and those lakes smaller than Buttermere, having been omitted. The lakes considered vary in length from 10·5 miles (16·8 kilom.) (Windermere) to 1·26 miles (2 kilom.) (Buttermere), and have mean breadths of from 0·5 to 0·25 miles (0·8 to 0·4 kilom.). They lie at uniformly low altitudes, Hawes Water, 694 feet (211 m.), being the highest.

During the past three years a considerable number of plankton collections have been made in the larger English lakes with the object of ascertaining more precisely the composition of their phytoplankton, its seasonal variations, and its relation to the physical characters of the lakes and their environment. This work was primarily planned as a continuation of our survey of the lake vegetation. It was, however, quickly realized that there appeared to be a close connection between the characters of the lake-basins, the rooted vegetation, and the phytoplankton (**2**), and it accordingly became desirable to develop the collections of phytoplankton on a comparative basis and, if possible, to make them quantitative.

The first account of the plankton vegetation of these lakes by W. and G. S. West (**5**) was to a very large extent confined to a description of the characteristic species of the lake area as a whole. The Wests, however, only took one collection from most of the lakes, although they subsequently studied the periodicity—for a year—in Wastwater, Ennerdale, and Windermere (**6**). No collections were made by these authors in Coniston and

Esthwaite. Our survey included the five lakes mentioned and also Buttermere, Crummock Water, Derwentwater, Bassenthwaite, Ullswater, and Hawes Water, and was only made possible by a series of grants from the Royal Society.

*Methods.*—As it was desired to make the descriptions of the lake plankton comparative, arrangements were made to take the collections from the different lakes at nearly the same time. Bad weather and other difficulties interfered with this idea somewhat, but, excepting Wastwater and Hawes Water (eight collections only), nine sets of comparative samples were taken from each of the eleven lakes—each of these sets being taken from the different lakes within a fortnight of one another, usually within a week. Thus the nine sets of comparative samples represent the following periods in each lake:—August 1920; April, July, August, late October 1921; May, July, September, November 1922. These samples—amplified by numerous additional collections from some of the lakes (see beginning of Table I.)—form the basis of all the subsequent account.

The samples were collected by towing a fine silk net (60 meshes per cm.) for half an hour at the surface of the lake and at an approximately uniform speed. Owing to the scarcity of plankton in many of these lakes, vertical hauls proved to be impracticable, although they were frequently tried. Indeed, in Wastwater, the surface haul had usually to be extended to one hour before any appreciable material could be collected. This method of collecting material precludes any very exact quantitative statement of the results, although owing to the inaccuracy of the usual counting method, probably little is lost by it. Each sample was first examined when fresh to facilitate the identification of Chlorophyceæ. At the same time at least five hundred organisms (usually one to two thousand) were counted, and the percentage composition of the phytoplankton was determined from the figures so obtained. The samples were examined independently by the two authors, and the lists checked in this way.

## I. DESCRIPTION.

In describing the phytoplankton community of a lake, it is necessary to make allowance for its seasonal and other variations. This can only be done when the characteristic species are judged by two criteria—*abundance* and *constancy*. The conditions for plankton organisms in a given lake presumably vary around a mean environment, which must favour the development of some organisms more than others. If the range of external conditions in the lake is never too extreme for the favoured organisms, these will persist and will be found in all collections—*i. e.*, they will be *constant* species. It must be supposed in such a case that the range of conditions in the given lake approaches closely the range for the ideal environment of the favoured organisms.

Commonly—as an examination of Table I. will show—the *constant* species are also most abundant, though this is not necessarily always the case, as the plant may sink too rapidly or divide too slowly ever to be present in any great quantity. On the other hand, some plants will be able to appear in a given lake only when the lake environment is at the extreme end of its range in one direction. Such plants are likely to be temporary, though they may be so abundant as to dominate the plankton when present. Their value as indicator species in describing a lake plankton is obviously less than that of the constant species, though they cannot be neglected, as they may throw light on the variability of the environment. As an example of these species, we may cite the extreme case of *Aphanizomenon*, which made up 70 % of the whole phytoplankton of the Esthwaite collection in November 1920, but which has only occurred in two collections out of 27 taken from this lake.

In the table of distribution we have attempted to record the abundance and constancy of the species observed in any lake. Where figures are given, they indicate percentages, those on the *left* hand the *maximum percentage of abundance* of the species in question, relative to the whole number of plants in the same collection ; those on the *right* hand the *percentage of relative constancy* of the species in the nine samples compared. These constancies are given to the nearest five per cent., as they are based only on nine samples. For some lakes, however, we have a larger number of collections, and in these cases there is very close agreement between the constancy based on the 9 comparative samples and that based on the larger number.

In Esthwaite, for example, with 27 samples the divergence—with one exception—is less than five per cent. Constancies are not given if the plant occurred in less than one-third of the samples. Where only one figure is given in the table, it represents maximum abundance. Plants recorded by the Wests—but not seen by us—are marked by W.

The distribution of the species observed is given in the following table (I.), from which the general phytoplankton type of each lake can be ascertained. Species occurring only as isolated specimens in a single lake are not included.

TABLE I.

| | WA. | EN. | BU. | CR. | HA. | DE. | BA. | CO. | WI. | ULL. | ES. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Samples examined { West | 13 | 13 | 1 | 1 | 1 | 1 | 1 | ... | 13 | 2 | ... | 46 |
| Samples examined { Pearsall | 8 | 14 | 9 | 9 | 8 | 10 | 9 | 12 | 23 | 17 | 27 | 146 |
| CHLOROPHYCEÆ. | | | | | | | | | | | | |
| *Mougeotia elegantula* Wittr. | ... | ... | ... | + | ... | + | 66/100 | + | | | | |
| *Gonatozygon Brebissonii* De Bary | + | + | ... | + | + | | | | | | | |
| ,, *Kinahani* (Arch.) Rabenh. | .. | –/30 | –/35 | ... | + | + | | | | | | |
| ,, *monotænium* De Bary | 4/35 | 15/90 | 1/90 | 4/75 | 2/75 | 1/80 | 1/35 | 6/50 | –/35 | + | + | |
| *Genicularia elegans* West | 2/35 | 38/80 | 1/45 | + | 2/75 | + | –/35 | ... | + | | | |
| *Cylindrocystis Brebissonii* Menegh. | ... | + | + | ... | + | ... | ... | + | | | | |
| ,, *diplospora* Lund. | + | + | + | + | + | + | | | | | | |
| *Penium Libellula* (Focke) Nordst. | ... | + | + | + | ... | ... | ... | ... | + | | | |
| ,, *minutum* (Ralfs) Cleve | ... | + | + | ... | ... | ... | ... | ... | + | | | |
| *Closterium acerosum* (Schrank) Ehrenb. | ... | ... | ... | ... | + | + | ... | ... | + | | | |
| ,, *Ehrenbergii* Menegh. | ... | ... | ... | + | + | ... | + | | | | | |
| ,, *Kutzingii* Bréb. | + | 1/30 | 3/45 | –/55 | + | 2/30 | 2/35 | ... | + | ... | + | |
| ,, *Lunula* (Müll.) Nitzsch | + | + | ... | ... | ... | ... | + | ... | + | ... | + | |
| ,, *moniliferum* (Bory) Ehrenb. | ... | ... | + | ... | ... | ... | ... | ... | + | ... | + | |
| ,, *parvulum* Naeg. | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | + | |
| ,, *setaceum* Ehrenb. | ... | + | + | + | ... | + | + | ... | ... | ... | + | |
| ,, *sigmoideum* Lagerh. & Nordst. | ... | ... | + | + | | | | | | | | |
| ,, *striolatum* Ehrenb. | ... | ... | ... | + | ... | ... | + | ... | + | | | |
| ,, *tumidum* Johnson | ... | W. | ... | ... | ... | ... | ... | ... | ... | ... | + | |
| *Pleurotænium coronatum* Bréb., var. *fluctuatum* West | ... | + | ... | + | –/75 | + | + | | | | | |
| ,, *Ehrenbergii* (Ralfs) De Bary | + | + | + | + | –/50 | + | + | ... | ... | ... | + | |
| ,, *Trabecula* (Ehrenb.) Naeg. | ... | + | + | ... | + | | | | | | | |
| *Euastrum ansatum* Ralfs | ... | + | + | + | ... | ... | + | ... | + | | | |
| ,, *elegans* Kütz. | ... | ... | + | + | + | + | | | | | | |
| ,, *verrucosum* Ehrenb., var. *reductum* Nordst. | ... | 1/30 | + | ... | + | + | + | ... | + | ... | + | |
| *Micrasterias Americana* Ehrenb. | + | ... | + | + | ... | ... | + | 12/40 | ... | ... | + | |
| ,, *apiculata* Menegh. | + | + | ... | ... | ... | + | | | | | | |
| ,, *Crux-Melitensis* (Ehrenb.) Hass. | ... | + | ... | ... | ... | ... | ... | ... | + | ... | + | |
| ,, *denticulata* Bréb. | + | + | ... | + | + | ... | + | + | | | | |
| ,, *mahabuleshwarensis* Hobs., var. *Wallichii* (Grun.) West | + | ... | + | 2/25 | +(2) | + | 18/100 | ... | + | ... | + | |
| ,, *papillifera* Bréb. | ... | –/30 | ... | + | ... | ... | ... | + | + | ... | + | |
| ,, *pinnatifida* (Kütz.) Ralfs | ... | W. | ... | ... | ... | ... | + | | | | | |
| ,, *radiata* Hass. | ... | ... | ... | + | ... | –/80 | + | ... | + | ... | + | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Micrasterias rotata* (Grev.) Ralfs | ... | + | 3/45 | –/45 | ... | + | –/55 | 31/65 | + | | |
| ,, *Sol* (Ehrenb.) Kütz. | + | –/60 | + | + | + | –/40 | + | ... | + | | |
| *Cosmarium abbreviatum* Racib., var. *planctonicum* West | ... | 1/30 | + | + | –/35 | + | + | + | + | –/35 | + |
| ,, *bioculatum* Bréb. | + | + | + | ... | 4/75 | –/50 | + | + | + | + | + |
| ,, *Botrytis* Menegh. | W. | + | + | + | –/60 | + | + | + | + | ... | –/35 |
| ,, *contractum* Kirchn. | ... | + | + | + | + | + | | | | | |
| ,, *cyclicum* Lund. | ... | ... | ... | ... | ... | + | ... | + | | | |
| ,, *depressum* (Naeg.) Lund. | W. | + | ... | + | –/50 | + | ... | ... | + | ... | –/45 |
| ,, *globosum* Bulnh. | ... | + | + | | | | | | | | |
| ,, *impressulum* Elfv. | ... | ... | ... | ... | + | ... | ... | ... | ... | ... | + |
| ,, *laeve* Rabenh. | ... | ... | ... | ... | + | ... | ... | + | | | |
| ,, *logiense* Bissett | ... | + | + | ... | ... | ... | ... | ... | ... | ... | + |
| ,, *margaritiferum* Menegh. | ... | ... | + | ... | + | ... | + | | | | |
| ,, *moniliforme* (Turp.) Ralfs | ... | ... | ... | ... | + | ... | ... | + | + | | |
| ,, *punctulatum* Bréb. | W. | ... | + | + | 1/50 | ... | ... | ... | ... | ... | + |
| ,, *reniforme* (Ralfs) Arch. | ... | + | ... | ... | + | ... | ... | + | + | + | + |
| ,, *subarctoum* (Lagerh.) Racib. | ... | 7/50 | ... | + | + | ... | + | | | | |
| ,, *subcostatum* Nordst. | ... | + | + | ... | + | ... | ... | ... | + | | |
| ,, *subcrenatum* Hantzsch | ... | + | 5/35 | + | + | + | ... | + | + | + | + |
| ,, *subtumidum* Nordst., var. *Klebsii* (Gutw.) West | ... | + | + | + | 3/35 | /40 | .. | + | + | ... | + |
| ,, *Turpinii* Bréb. | ... | ... | + | ... | ... | ... | ... | ... | + | ... | + |
| *Xanthidium antilopeum* (Bréb.) Kütz. | + | 1/80 | + | + | 1/100 | –/60 | –/65 | ... | + | + | + |
| ,, ,, var. *depauperatum* West | ... | ... | 4/55 | 2/75 | + | + | ... | ... | ... | 1/80 | |
| ,, ,, var. *triquetrum* Lund. | ... | ... | ... | + | .. | /50 | + | | | | |
| ,, *armatum* (Bréb.) Rabenh. | + | + | + | | | | | | | | |
| ,, *subhastiferum* West, var. *Murrayi* West | + | ... | ... | ... | –/35 | ... | ... | ... | 8/70 | | |
| *Arthrodesmus crassus* West | ... | 4/70 | ... | ... | 3/75 | + | | | | | |
| ,, *Incus* (Bréb.) Hass. | + | 4/50 | 1/35 | ... | + | 2/60 | 2/35 | | | | |
| ,, *triangularis* Lagerh. | ... | 1/60 | + | + | ... | + | | | | | |
| *Staurastrum anatinum* Cooke & Wills | + | 4/80 | 12/90 | 3/65 | + | + | + | + | + | | |
| ,, *Arctiscon* (Ehrenb.) Lund. | + | 10/100 | –/45 | 2/75 | 2/75 | 5/80 | 2/75 | ... | + | ... | + |
| ,, *brachiatum* Ralfs | + | ... | ... | ... | ... | + | | | | | |
| ,, *brasiliense* Nordst., var. *Lundellii* W. & G. S. West | ... | 7/90 | + | ... | ... | 1/80 | + | | | | |
| ,, *brevispinum* Bréb., f. *major* West | ... | + | ... | ... | –/50 | ... | ... | ... | ... | + | |
| ,, *curvatum* West | + | + | + | 1/55 | 2/75 | ... | W. | ... | 4/50 | + | + |
| ,, *cuspidatum* Bréb., var. *maximum* West | W.-/65 | ... | + | –/44 | ... | + | W. | ... | –/55 | 4/60 | |
| ,, *dejectum* Bréb. | ... | –/35 | ... | + | W. | ... | ... | ... | ... | + | |
| ,, *denticulatum* (Naeg.) Arch. | + | 3/35 | ... | ... | 5/75 | –/60 | + | ... | + | | |
| ,, *furcigerum* Bréb. | + | + | ... | + | + | | | | | | |
| ,, *gracile* Ralfs | ... | ... | + | ... | ... | ... | + | ... | + | | |
| ,, *grande* Bulnh. | ... | ... | ... | ... | –/50 | –/60 | + | | | | |
| ,, *granulosum* (Ehrenb.) Ralfs, f. | ... | ... | ... | ... | –/50 | + | + | ... | –/35 | –/45 | 3/50 |

| | WA. | EN. | BU. | CR. | HA. | DE. | BA. | CO. | WI. | ULL. | ES. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Staurastrum jaculiferum* West | 75/100 | 5/30 | 16/100 | 7/90 | 1/85 | + | + | ... | 5/70 | 4/80 | + |
| ,, *longispinum* (Bail.) Arch. | ... | 84/100 | + | ... | ... | 2/70 | + | | | | |
| ,, *lunatum* Ralfs, var. *planctonicum* West | + | –/40 | + | –/55 | 1/75 | –/40 | –/45 | ... | 2/55 | –/35 | + |
| ,, *megacanthum* Lund., var. *scoticum* West | ... | W. | ... | ... | + | ... | | | | | |
| ,, *Ophiura* Lund. | ... | + | ... | ... | ... | 1/90 | + | | | | |
| ,, *paradoxum* Meyen | + | –/40 | 1/65 | 2/90 | 2/50 | 1/50 | –/35 | + | 8/90 | + | 1/55 |
| ,, *polymorphum* Bréb. | ... | W. | ... | ... | ... | ... | + | | | | |
| ,, *pseudopelagicum* West | ... | ... | ... | + | ... | ... | ... | ... | 2/35 | | |
| ,, *punctulatum* Bréb., var. *pygmæum* West | ... | ... | 4/35 | + | + | + | + | + | | | |
| ,, *saxonicum* Bulnh. | ... | ... | ... | ... | ... | + | –/45 | | | | |
| ,, *sexangulare* (Bulnh.) Lund. | + | 2½/40 | ... | ... | ... | –/30 | | | | | |
| ,, *teliferum* Ralfs | ... | W. | ... | ... | + | ... | ... | ... | + | | |
| *Spondylosium pulchrum* (Bail.) Arch., var. *planum* Wolle | + | + | + | 34/75 | 8/100 | 9/100 | 2/90 | + | 2/75 | + | 5/90 |
| *Sphærozosma Aubertianum* West | ... | 1/50 | ... | + | ... | + | ... | ... | + | | |
| ,, *granulatum* Roy & Biss. | ... | W. | + | ... | –/35 | ... | + | | | | |
| ,, *vertebratum* Ralfs | 2/37 | + | ... | ... | + | + | | | | | |
| *Desmidium aptogonum* Bréb. | .. | + | ... | ... | ... | ... | ... | ... | W. | | |
| ,, *Swartzii* Ag. | + | + | ... | ... | ... | + | ... | ... | ... | ... | + |
| *Gymnozyga moniliformis* Ehrenb. | + | –/40 | | | | | | | | | |
| *Hyalotheca dissiliens* (Sm.) Bréb. | + | 7/60 | –/35 | –/35 | ... | + | + | . | + | ... | + |
| ,, *mucosa* Ehrenb. | 8/35 | –/60 | 2/65 | –/45 | + | –/40 | + | + | –/30 | ... | + |
| *Eudorina elegans* Ehrenb. | ... | + | + | 1/75 | 3/100 | 2/100 | –/65 | 2/40 | 22/70 | 1/65 | 24/95 |
| *Volvox mononæ* G. M. Smith | ... | ... | ... | ... | 2/35 | ... | ... | ... | 16/40 | ... | + |
| *Pandorina morum* Bory | ... | ... | ... | ... | + | ... | ... | ... | + | | |
| *Pediastrum Boryanum* (Turp.) Menegh. | ... | ... | ... | ... | –/50 | + | + | + | –/45 | + | –/35 |
| ,, *Tetras* (Ehr.) Ralfs | ... | ... | ... | ... | + | ... | ... | ... | ... | ... | + |
| *Crucigenia rectangularis* (A. Br.) Gay | ... | ... | ... | + | + | + | + | | | | |
| *Scenedesmus bijugatus* (Turp.) Kütz | ... | ... | ... | ... | 2/35 | + | + | ... | + | + | + |
| ,, *denticulatus* Lagerh., var. *linearis* Hansgirg | ... | ... | ... | ... | ... | ... | ... | + | ... | + | |
| ,, *obliquus* (Turp.) Kütz. | ... | ... | ... | + | ... | ... | + | | | | |
| ,, *quadricauda* (Turp.) Bréb. | ... | ... | ... | ... | ... | + | ... | ... | + | | |
| *Nephrocytium Agardhianum* Naeg. | ... | ... | + | ... | + | | | | | | |
| ,, *lunatum* W. West | ... | ... | ... | + | + | ... | .. | ... | W. | | |
| *Ankistrodesmus falcatus* (Corda) Ralfs | ... | + | 3/35 | + | + | + | ... | ... | + | + | + |
| ,, *Pfitzeri* (Schröd.) G. S. West | ... | ... | ... | 1/65 | ... | ... | ... | ... | ... | +(4) | |
| *Oocystis lacustris* Chodat | 4/35 | 2/30 | ... | + | + | ... | ... | ... | + | 14/60 | |
| ,, *parva* West | + | + | + | ... | ... | ... | ... | + | | | |
| *Elaktothrix gelatinosa* Wille | –/35 | ... | ... | ... | + | | | | | | |
| *Tetraedon quadratum* (Reinsch) Hansgirg | ... | ... | ... | + | ... | ... | ... | ... | ... | ... | + |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dictyosphærium pulchellum* Wood | ... | + | ... | + | + | + | + | ... | 3/50 | ... | + |
| *Sphærocystis Schroeteri* Chodat | 56/75 | 8/70 | 16/75 | 8/100 | 4/85 | 3/100 | + | 3/50 | 22/65 | 1/45 | –/50 |
| *Glœocystis gigas* (Kütz.) Lagerh. | 3/65 | 1/40 | 4/35 | 3/65 | -/65 | –/40 | –/35 | 46/90 | –/35 | 1/35 | + |
| ,, *planctonicum* Lemm. | + | ... | + | + | ... | ... | ... | ... | + | | |
| *Tetraspora lacustris* Lemm. | ... | ... | + | + | -/65 | 27/30 | + | + | + | + | + |
| *Botryococcus Braunii* Kütz. | ... | + | 33/90 | 15/75 | 10/50 | 4/80 | ... | ... | +(4) | + | + |
| *Chlorobotrys limneticus* G. M. Smith | ... | ... | + | ... | + | ... | ... | ... | ... | 12/20 | |
| *Schizochlamys delicatula* West | ... | ... | 1/35 | 6/45 | | | | | | | |
| BACILLARIEÆ. | | | | | | | | | | | |
| *Melosira granulata* Ehrenb. | –/35 | 3/30 | + | 2/35 | + | ... | + | + | 32/78 | 3/20 | 36/82 |
| *Cyclotella comta* (Ehrenb.) Kütz. | ... | 28/40 | ... | 3/35 | 1/35 | 2/70 | 10/35 | + | 6/75 | 1/60 | 10/45 |
| *Rhizosolenia morsa* W. & G. S. West | W. | W. | ... | 1/35 | ... | –/30 | ... | ... | 15/65 | ... | 5/40 |
| *Tabellaria fenestrata* (Lyngb.) Kütz. | 7/75 | 10/90 | 30/90 | 30/90 | 57/100 | 42/100 | 47/100 | 10/65 | 5/100 | 91/100 | 10/100 |
| ,, ,, var. *asterionelloides* Grunow | + | W. | –/35 | 37/75 | 3/50 | 2/50 | 4/80 | + | 34/100 | 24/65 | 3/60 |
| ,, *flocculosa* Kütz. | 12/100 | 6/100 | 12/100 | 4/100 | 3/100 | 2/100 | 12/100 | 38/100 | 1/90 | 4/100 | 2/82 |
| *Fragilaria capucina* Desmaz. | + | –/40 | –/55 | –/65 | + | ... | + | 5/75 | –/60 | + | 2/63 |
| ,, *virescens* Ralfs | ... | ... | + | + | ... | ... | ... | + | | | |
| *Diatoma elongatum* Agardh | ... | ... | + | ... | ... | ... | ... | ... | + | | |
| *Synedra Acus* Kütz. | –/65 | + | W. | + | 2/50 | + | –/35 | –/50 | + | W. | + |
| ,, *pulchella* Kütz. | W. | + | + | + | + | + | + | 8/40 | + | + | |
| ,, *radians* Kütz. | + | + | –/55 | + | + | + | + | + | + | + | + |
| ,, *Ulna* Ehrenb. | ... | + | –/35 | 2/45 | + | + | –/55 | 14/65 | –/35 | + | + |
| *Asterionella gracillima* (Hantzsch) Heiberg | 17/37 | 10/30 | 5/35 | 14/45 | 4/65 | 86/100 | 67/100 | 15/66 | 86/100 | 96/100 | 96/100 |
| *Ceratoneis Arcus* Kütz. | ... | ... | + | + | ... | ... | ... | ... | + | + | + |
| *Eunotia Arcus* Ehrenb. | ... | ... | ... | ... | + | ... | .. | ... | ... | + | + |
| ,, *gracilis* Ehrenb. | + | + | + | + | –/35 | ... | ... | +(3) | + | .. | + |
| ,, *lunaris* Ehrenb. | W. | + | + | ... | + | ... | ... | + | ... | ... | + |
| ,, *major* W. Sm. | ... | 3/30 | | | | | | | | | |
| ,, *pectinalis* Kütz. | + | + | + | | | | | | | | |
| ,, *robusta* Ralfs, var. *tetraodon* Ehrenb. | ... | + | ... | ... | ... | ... | ... | ... | ... | ... | + |
| *Cocconeis flexella* Kütz. | ... | + | + | + | ... | ... | ... | ... | ... | + | + |
| *Navicula alpina* W. Sm. | ... | +(3) | | | | | | | | | |
| ,, *cryptocephala* Kütz. | ... | + | + | ... | ... | ... | ... | ... | + | ... | + |
| ,, *divergens* W. Sm. | ... | +(3) | ... | ... | ... | ... | ... | ... | + | | |
| ,, *major* Kütz. | ... | + | ... | + | + | ... | + | + | + | + | + |
| ,, *oblonga* Kütz. | ... | ... | ... | ... | ... | ... | ... | .. | + | + | + |
| ,, *radiosa* Kütz. | ... | + | ... | ... | –/65 | ... | ... | ... | + | ... | + |
| ,, *rhomboides* Ehrenb | –/65 | 1/40 | –/35 | + | ... | + | ... | 9/35 | | | |
| ,, *Smithii* Bréb. | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | + |
| ,, *viridis* Ehrenb. | ... | ... | ... | ... | ... | + | + | ... | + | ... | + |

| | Wa. | En. | Bu. | Cr. | Ha. | De. | Ba. | Co. | Wi. | Ull. | Es. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Gyrosigma attenuatum* Kütz. | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | + |
| ,, *Kutzingii* Grunow | ... | + | ... | ... | ... | ... | .. | ... | + | ... | + |
| *Gomphonema acuminatum* Ehrenb. | ... | + | + | ... | ... | ... | ... | + | + | + | |
| ,, *geminatum* Lyngb. | W. | + | + | + | –/35 | + | ... | + | + | + | + |
| ,, *intricatum* Kütz. | + | –/40 | + | + | ... | ... | ... | ... | + | | |
| *Cymbella cymbiformis* Kütz. | + | + | ... | ... | - /85 | + | ... | + | + | + | + |
| ,, *gracilis* Rabenh. | + | + | + | + | + | ... | ... | ... | ... | ... | + |
| ,, *lanceolata* Ehrenb. | ... | + | ... | ... | –/35 | + | ... | ... | + | | |
| ,, *prostrata* Berkeley | ... | ... | ... | ... | + | ... | ... | .. | ... | ... | + |
| ,, *ventricosa* Kütz. | ... | + | ... | ... | + | ... | ... | ... | + | ... | + |
| *Amphora ovalis* Kütz. | ... | + | ... | + | –/35 | ... | ... | ... | + | ... | + |
| *Epithemia turgida* (Ehrenb.) Kütz. | + | ... | ... | ... | + | ... | ... | ... | + | ... | + |
| ,, *zebra* Ehrenb. | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | + |
| *Nitzschia linearis* (Agardh.) W. Sm. | ... | + | + | ... | + | ... | ... | + | + | + | + |
| ,, *palea* Kütz. | ... | ... | + | ... | ... | ... | + | ... | ... | ... | + |
| ,, *sigma* (Kütz.) W. Sm. | ... | + | ... | ... | ... | ... | ... | ... | + | | |
| ,, *sigmoidea* (Nitzsch) W. Sm. | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | + |
| *Stauroneis Phœnicenteron* Ehrenb. | ... | ... | ... | ... | + | ... | + | ... | + | ... | + |
| *Amphipleura pellucida* Kütz. | ... | ... | ... | ... | ... | + | ... | ... | + | + | |
| *Surirella biseriata* Bréb. | + | 15/60 | + | + | + | ... | + | ... | + | + | + |
| ,, *elegans* Ehrenb. | ... | ... | ... | ... | ... | ... | ... | ... | ... | + | + |
| ,, *linearis* W. Sm. | ... | + | + | ... | ... | + | ... | ... | + | ... | + |
| ,, *ovalis* Bréb. | W. | + | + | ... | ... | ... | ... | ... | ... | ... | + |
| ,, *robusta* Ehrenb. | –/65 | 9/40 | ... | + | + | + | + | 10/75 | 2/55 | + | –/45 |
| ,, ,, Ehrenb., var. *splendida*, Kütz. | ... | 8/80 | ... | ... | + | + | + | ... | + | ... | + |
| *Campylodiscus hibernicus* Ehrenb. | ... | + | ... | ... | ... | ... | ... | ... | + | ... | + |
| Myxophyceæ. | | | | | | | | | | | |
| *Anabæna circinalis* (Kütz.) Hansg. | ... | ... | + | + | ... | ... | ... | ... | + | ... | 30 35 |
| ,, *Flos-aquæ* (Lyngb.) Bréb. | ... | ... | ... | ... | 8/50 | ... | ... | ... | + | ... | 38/65 |
| ,, *Lemmermanni*, P. Richter | ... | ... | ... | ... | 20 75 | 40/80 | –/35 | ... | 38/55 | + | 30/75 |
| *Aphanizomenon Flos-aquæ* (L.) Ralfs | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | 70/– |
| *Oscillatoria Agardhii* Gomont | ... | + | +(7) | /55 | 1/35 | –/30 | + | 14/50 | 16/85 | –/40 | 69/95 |
| ,, *rubescens* DC. | ... | .. | ... | ... | ... | ... | ... | ... | + | ... | + |
| ,, *tenuis* Ag. | ... | + | –/35 | ... | + | ... | + | ... | + | + | 22/35 |
| *Merismopedia glauca* (Ehr.) Naeg. | W. | + | + | + | + | + | ... | + | + | + | |
| *Cœlosphærium Kutzingianum* Naeg. | ... | ... | +(1) | 26/65 | 52/85 | ... | + | ... | 40/71 | –/35 | 76/90 |
| ,, *Nægelianum* Unger | ... | ... | ... | + | + | + | + | ... | + | ... | + |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Microcystis æruginosa* Kütz. | ... | ... | ... | + | ... | + | ... | ... | + | ... | + |
| ,, *Flos-aquæ* (Wittr.) Kirchn. | ... | ... | ... | + | + | ... | ... | ... | 6/50 | ... | 3/65 |
| ,, *pulvera* (Wood) Migula | ... | ... | + | ... | ... | -/50 | ... | ... | + | ... | + |
| *Gomphosphæria lacustris* Chodat | + | + | -/35 | + | -/50 | + | ... | ... | ... | ... | + |
| *Chroococcus limneticus* Lemm. | ... | ... | + | ... | + | ... | ... | ... | ... | +(4) | |
| ,, *turgidus* (Kütz.) Naeg. | ... | + | ... | ... | + | ... | ... | ... | ... | + | |
| *Aphanocapsa delicatissima* W. & G. S. West | + | + | + | | | | | | | | |
| ,, *elachista* Naeg. | ... | ... | ... | + | -/35 | + | ... | ... | + | + | + |
| *Aphanothece nidulans* P. Richter | ... | ... | ... | ... | + | ... | ... | ... | ... | ... | + |
| ,, ,, ,, var. *endophytica* West | ... | ... | ... | + | + | ... | ... | ... | + | ... | + |
| ,, *stagnina* (Sprengel) A. Braun | ... | + | ... | ... | ... | ... | ... | ... | + | ... | + |
| PHÆOPHYCEÆ. | | | | | | | | | | | |
| *Mallamonas longiseta* Lemm. | ... | ... | ... | ... | ... | ... | ... | ... | 1/35 | + | + |
| *Dinobryon crenulatum* W. & G. S. West | + | W. | ... | + | | | | | | | |
| ,, *cylindricum* Imhof | ... | 5/30 | + | 68/35 | 66/37 | + | + | ... | + | + | |
| ,, *divergens* Imhof | W. | 4/30 | 90/100 | 50/75 | 30/50 | 75/100 | 10/65 | + | 20/35 | 29/55 | 30/35 |
| ,, *stipitatum* Stein | ... | -/40 | ... | ... | ... | +(2) | +(3) | ... | + | | |
| ,, *bavaricum* Imhof | ... | ... | ... | + | ... | -/40 | ... | ... | ... | ... | +(3) |
| PERIDINIEÆ. | | | | | | | | | | | |
| *Peridinium cinctum* (Müller) Ehrenb. | ... | ... | + | ... | ... | ... | ... | ... | ... | ... | +(2) |
| ,, *inconspicuum* Lemm. | ... | + | ... | ... | + | ... | ... | ... | ... | ... | + |
| ,, *Willei* Huitf.-Kaas | 1/100 | 10/80 | 10/100 | 1/75 | + | 5/50 | + | + | 2/55 | + | 3/50 |
| *Ceratium Hirundinella* (O. F. Muell.) Schrank | +(2) | 3/30 | 1/45 | -/75 | 7/100 | 2/80 | 1/45 | 83/75 | 5/75 | + | 20/55 |

In TABLE I. and the subsequent tables and descriptions the following abbreviations are used to indicate the various lakes:—

| | | | | | |
|---|---|---|---|---|---|
| Wastwater | WA. | Hawes Water | HA. | Ullswater | ULL. |
| Ennerdale | EN. | Derwentwater | DE. | Windermere | WI. |
| Buttermere | BU. | Bassenthwaite | BA. | Esthwaite | ES. |
| Crummock | CR. | Coniston | CO. | | |

## II. ANALYSIS OF RECORDS.

In attempting to analyse more fully the common or dissimilar features of the various lakes, we have considered only the simplest comparisons, for a detailed numerical analysis would press the statistical side of these observations far beyond any ecological or other interpretation which can possibly be attempted at present. There appear to be three direct and simple methods of comparing the planktons of the various lakes. The comparisons may be based (i.) on the dominant or most abundant species (ii.) on the constant species, (iii.) on the average percentage composition of the planktons at the times of collection.

The dominant species are given in Table II. In this, **d** indicates species which (in the given lake) at times make up more than 66 $^0/_0$ of the whole phytoplankton. Species whose maximum abundance lies between 33–66 $^0/_0$ are given as sub-dominant, *sd*. The table, therefore, includes all species forming more than 33 $^0/_0$ of the phytoplankton at any time.

TABLE II.—*Dominant Species.*

| | Wa. | En. | Bu. | Cr. | Ha. | De. | Ba. | Ull. | Wi. | Es. |
|---|---|---|---|---|---|---|---|---|---|---|
| *Asterionella gracillima* ............ | .. | .. | .. | .. | .. | **d** | **d** | **d** | **d** | **d** |
| *Melosira granulata* ................ | .. | .. | .. | .. | .. | .. | .. | .. | *sd* | *sd* |
| *Tabellaria fenestrata* and var. ...... | .. | .. | *sd* | *sd* | *sd* | *sd* | *sd* | **d** | *sd* | |
| *Cœlosphærium Kützingianum*........ | .. | .. | .. | .. | *sd* | .. | .. | .. | **sd* | **d** |
| *Oscillatoria Agardhii* .............. | .. | .. | .. | .. | .. | .. | .. | .. | .. | **d** |
| *Anabæna* spp. ..................... | .. | .. | .. | .. | .. | *sd* | .. | .. | *sd* | *sd* |
| *Dinobryon* spp...................... | .. | .. | **d** | **d** | ***d** | **d** | | | | |
| *Mougeotia elegantula* .............. | .. | .. | .. | .. | .. | .. | **d** | | | |
| *Staurastrum jaculiferum* .......... | **d** | .. | | | | | | | | |
| „ *longispinum*............ | .. | **d** | | | | | | | | |
| Green sub-dominants ............... | s | g | b | sp | | | | | | |

b = *Botryococcus Braunii.*
g = *Genicularia elegans.*
s = *Sphærocystis Schroeteri.*
sp = *Spondylosium planum.*

In the above table the 2 species asterisked are present in less than 75 $^0/_0$ of the samples and are, therefore, relatively temporary, but the others are practically constant species. Coniston is omitted from Table II. on account of its fragmentary plankton. The full figures upon which this table is based are readily obtained from Table I., and they can be amplified as far as is desired. Further analysis, however, adds no facts of great importance to the above table. It will be seen that the first two lakes—Wastwater and Ennerdale—are dominated by Desmids, the next four by *Dinobryon*, and the last five have *Asterionella* dominant at times.

The distribution of the sub-dominant diatoms and green algæ, on the whole, runs parallel to the main features just described, but *Mougeotia elegantula*—at times dominant in Bassenthwaite—seems to suggest that this lake has affinities with Wastwater or Ennerdale. The dominance of the two diatoms, *Asterionella* and *Tabellaria fenestrata*, however, indicates a much closer relation to the other diatom lakes.

While the dominant Myxophyceæ show increase roughly toward the right-hand end of the table, it is clear from their rather sporadic distribution that the environmental factors inducing abundance of these algæ are not necessarily the same as those governing the distribution of the Chlorophyceæ, *Dinobryon*, or Diatoms, though they may be similar.

The constant species tend to vary from lake to lake, but the dominant species given in Table II. are for the most part also constant. Table III. is a summary giving the number of species (in each of the main groups) which are present in more than 75 % of the collections from a given lake.

TABLE III.—*Constant Species.*

| | Wa. | En. | Bu. | Cr. | Ha. | De. | Ba. | Ull. | Wi. | Es. | Co. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Desmids (Conjugatæ) .......... | 1 | 7 | 3 | 6 | 12 | 7 | 4* | 2 | 2 | 1 | |
| Colonial Chlorophyceæ ........ | 1 | .. | 2 | 3 | 2 | 3 | .. | .. | 1 | 1 | 1 |
| Diatoms (excluding *Tabellaria*) .. | .. | 1 | .. | .. | 1 | 1 | 1 | 2 | 3 | 2 | 1 |
| Myxophyceæ ................ | .. | .. | .. | .. | 2 | 1 | .. | .. | 1 | 3 | |
| Peridinieæ ................ | 1 | 1 | 1 | 2 | 1 | 1 | .. | .. | 1 | .. | 1 |
| *Dinobryon* ................ | .. | .. | 1 | 1 | .. | 1 | .. | .. | .. | .. | |

* Including *Mougeotia elegantula.*

The two Diatoms, *Tabellaria flocculosa* and *T. fenestrata*, are constant in every lake except Coniston, where the latter of the pair is rather sporadic. Hence these two species, being of little comparative significance, are excluded. *Cyclotella comta* is constant in Ullswater and Windermere, and *Melosira granulata* in Windermere and Esthwaite.

Of the Peridinieæ, *Peridinium Willei* is constant in the first four lakes, and *Ceratium Hirundinella* in the others indicated. Of the Colonial Green Algæ, *Sphærocystis Schroeteri* tends to be more constant in the left-hand lakes, and *Eudorina elegans* toward the right-hand of the series.

Excluding the two Tabellariæ as being of no significance here, it is clear that *Dinobryon*, *Peridinium Willei*, and the Green Algæ include the majority of the constant species in the first six lakes, while in the remaining lakes *Ceratium*, Diatoms, and Myxophyceæ provide a much greater proportion of the constant species. The conclusions drawn from this table are therefore essentially similar to those drawn from Table II., although in the present case many of the species never attain any marked abundance. Moreover, from Table II. we should suspect that the first two lakes in the series represent conditions favourable for one set of organisms (Chlorophyceæ), while the last three or four represent conditions favouring another set (*e.g.* Diatoms). The intermediate lakes should, therefore, tend to have intermediate conditions between these two extremes, and therefore to contain the largest numbers of constant species. This is shown to be the case in Table III.

The average percentage composition of the phytoplankton of the various lakes is given in Table IV., the figures being based on the nine comparative samples previously mentioned.

TABLE IV.—*Average Percentage Composition.*

| | Wa. | En. | Bu. | Cr. | Ha. | De. | Ba. | Co. | Wi. | Ull. | Es. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Chlorophyceæ: | | | | | | | | | | | |
| (1) Filamentous | 12 | 5½ | 7 | 2 | 2 | 2 | 27 | 10 | ½ | .. | 1 |
| (2) Colonial | 27 | 4 | 15 | 10 | 7 | 3½ | 2 | 14 | 8½ | 4 | 6 |
| (3) Desmids | 41 | 70 | 18 | 17 | 15 | 5 | 8½ | 7 | 7 | 3½ | 2 |
| *Dinobryon* | .. | 1 | 36 | 32 | 14½ | 37 | 1 | .. | 2½ | 2½ | 3 |
| Peridinieæ | 5 | 2½ | 6 | 1 | 5 | 1 | ½ | 20 | 1 | .. | 3 |
| *a.* Total | 85 | 83 | 82 | 62 | 43½ | 48½ | 39 | 51 | 19½ | 10 | 15 |
| Bacillariæ | 14 | 15 | 15 | 25 | 30 | 44½ | 60 | 45 | 60½ | 87 | 33 |
| Myxophyceæ | ½ | 1 | 3 | 12 | 26 | 6 | ½ | 3 | 18 | 2½ | 51 |
| *b.* Total | 14½ | 16 | 18 | 37 | 56 | 50½ | 60½ | 48 | 78½ | 89½ | 84 |
| Group I. | 85 | 83 | 82 | 62 | 39½ | 48 | 38½ | 31 | 18½ | 10 | 13 |
| Group II.* | 14½ | 16 | 18 | 37 | 60 | 51 | 61 | 68 | 79½ | 89½ | 86 |

* Including *Ceratium* from Total *a.*

These figures are less easy to interpret, but if—on the basis of Table III.—the percentage of *Peridinium*, *Dinobryon*, and Chlorophyceæ be determined (Group I.) in contrast with the percentage of Myxophyceæ, Diatoms, and *Ceratium* (Group II.), it will be found that there is a fairly regular progression from the lakes with a high average percentage of Chlorophyceæ and Flagellates, to those with Diatoms and Myxophyceæ predominant. The discrepancies in this general progression (high Chlorophyceæ in Bassenthwaite, high Myxophyceæ in Crummock and Hawes W.) are obviously of minor importance in attempting a general statement, for it is unlikely that any one environmental factor will affect the distribution of all these diverse types of organisms.

On the other hand, it has already been demonstrated (Pearsall, 2) that the environmental conditions in these lakes show a definite progression from lakes of the Wastwater-Ennerdale type to those like Esthwaite, the order of progression being that employed in the tables. Wastwater and Ennerdale are rocky lakes, with relatively coarse sediments, and lying amid rocky and uncultivated surroundings. Their waters are clear, very poor in dissolved substances and particularly in calcium salts, nitrates, and silica. Esthwaite is a silted lake, with relatively fine sediments and lying in soil-covered and more cultivated country. Its waters are rather turbid, richer in dissolved calcium salts, in nitrates, and in silica—to a less extent Windermere and Ullswater are similar. The remaining lakes are intermediate between these two extremes, roughly in the order given in the tables. The original grouping of these lakes was based entirely on their physical characteristics together with the character of their rooted vegetation, and it is significant that the analysis of their phytoplankton should give groupings so closely similar.

## III. The Phytoplankton Associations.

So far, the analysis attempted has dealt with the major taxonomic groups of plankton organisms. It is, however, fairly obvious that one may have *species constantly occurring together* and forming easily recognized *associations*, although the associated species belong to widely different natural orders. These associations are characterized most easily by their dominant species, and in the sense used here, the term association refers to the associated species which are constantly present along with a given dominant or dominants. In determining the following associations we have been faced with the difficulty that the plankton of these lakes is often very mixed, with no clearly defined dominant. We have, therefore, taken a low limit of dominancy (33 %) as the basis for the following descriptions. In determining, for example, the composition of the *Tabellaria fenestrata* association, all samples from any lakes were taken in which *Tabellaria fenestrata* formed over 33 % of the whole plankton. The constancy of the remaining species *in these samples* was then determined. One species (*Asterionella*) occurs in over 90 % of these samples, and is hence a *constant* member of the association. Other species (*Eudorina elegans*, *Staurastrum jaculiferum*, *Xanthidium antilopeum*) which occur in more than 66 % of the given samples are usually—but not always—present. These are referred to as *sub-constant* species. This method obviously expresses in the simplest way a correlation coefficient between the dominant species and those associated with it in nature.

The following associations have been recognized; and most of them can be recognized when the dominants form less than 33 % of the whole plankton.

**Chlorophycean** association complex.

(1) **Staurastrum jaculiferum–Sphærocystis Schroeteri** association.

Sub-constant : *Peridinium Willei* and *Glœocystis gigas.*

Occurring in Wa., En., Bu. A similar association occurs in Ha., Wi., Ull.—but is never dominant.

(2) **Staurastrum longispinum–Genicularia elegans** association.

Constant : *Gonatozygon monotænium*, *Staurastrum brasiliense, S. Arctiscon.*

Sub-constant : *Xanthidium antilopeum*, *Sphærocystis Schroeteri*, *Peridinium Willei.*

Well-developed only in Ennerdale ; occurs also in De. The rarer desmids, *Staurastrum Ophiura, S. anatinum, Arthrodesmus Incus*, and *A. crassus*, probably belong to this association.

(3) **Mougeotia elegantula–Micrasterias Wallichii** association.

Sub-constant : *Xanthidium antilopeum*, *Staurastrum saxonicum, S. Arctiscon, Spondylosium planum, Dinobryon cylindricum.*

Occurs in Bassenthwaite only.

(4) **Spondylosium planum—Eudorina elegans** association.

Constant : *Tabellaria fenestrata, Asterionella gracillima.*

Sub-constant : *Staurastrum paradoxum, Ceratium Hirundinella, Dinobryon cylindricum, Oscillatoria Agardhii, Cœlosphærium Kutzingianum.*

Occurs in Cr., Wi., Es.–not dominant, but recognizable in Ha. and De.

(5) **Dinobryon** association.

Constant : *Tabellaria fenestrata, Botryococcus Braunii, Spondylosium planum.*

Sub-constant : *Sphærocystis Schroeteri, Peridinium Willei, Ceratium Hirundinella, Eudorina elegans, Closterium Kutzingii, Staurastrum Arctiscon, S. jaculiferum.*

Occurs in Bu., Cr., Ha., De. ; also recognizable, though not dominant, in Wi., Ull., Ba., and Es.

(6) **Dinobryon–Botryococcus** association.

The two species approximately co-dominant, together + 33 %.

Constant : *Sphærocystis Schroeteri, Xanthidium antilopeum, Staurastrum jaculiferum, Gonatozygon monotænium.*

Sub-constant : *Glœocystis gigas, Spondylosium planum, Hyalotheca mucosa, Staurastrum paradoxum, S. anatinum, S. Arctiscon, Genicularia elegans, Tabellaria fenestrata, Peridinium Willei, Ceratium Hirundinella.*

This is a typical summer phase in a *Dinobryon* lake. The constants are so different that we have felt bound to separate it from the *Dinobryon* association. Occurs in Bu., Cr., Ha.

### **Diatom** associations.

(7) **Tabellaria fenestrata** association.

Constant: *Asterionella gracillima.*

Sub-constant: *Eudorina elegans*, *Staurastrum jaculiferum*, *Xanthidium antilopeum.*

In Bu., Cr., Ha., De., Ba., Ull.

(8) **Asterionella gracillima** association.

Constant: *Tabellaria fenestrata.*

Sub-constant: *Cyclotella comta*, *Oscillatoria Agardhii*, *Eudorina elegans*, *Spondylosium planum*, *Staurastrum paradoxum.*

(8*a*) **Melosira** variant of **Asterionella** association (*Melosira* over 10 % of whole plankton) has in addition :—

Constant: *Oscillatoria Agardhii* and *Cœlosphærium Kutzingianum.*

Sub-constant: *Mallomonas longiseta.*

In Windermere and Esthwaite.

### **Myxophycean** associations.

(9) **Oscillatoria Agardhii** association.

Constant: *Ceratium Hirundinella.*

Sub-constant: *Eudorina elegans*, *Spondylosium planum.*

Occurs in Esthwaite ; present but not dominant in Co., Wi.

(10) **Cœlosphærium Kutzingianum** association.

Constant: *Asterionella gracillima*, *Eudorina elegans*, *Tabellaria fenestrata*, *Spondylosium planum.*

Sub-constant: **Oscillatoria Agardhii*, *Anabæna Lemmermanni*, **Staurastrum paradoxum*, *Ceratium Hirundinella.*

Occurs in Cr., Ha., Wi., Es.

(11) **Anabæna** spp. association.

This association is strikingly similar to the last (10), and contains the same constants (with the same constancy). The sub-constants are the two asterisked in 10, with *Sphærocystis Schroeteri* and *Botryococcus Braunii* in addition.

Found in Ha., De., Wi., Es.

(12) **Aphanizomenon Flos-aquæ** association.

Once seen in Esthwaite only. Associates doubtful—probably *Ceratium Hirundinella.*

The ecological conditions under which these associations occur will be dealt with in subsequent communications.

## IV. NOTEWORTHY SPECIES.

The scarcity of new records of species—in spite of the large number of samples taken and the care with which they have been examined—is a striking testimony to the thoroughness of the primary survey carried out by the late W. and G. S. West. Some of the species given in our list they did not obtain from the lakes, but from the smaller tarns. Both *Dinobryon cylindricum* and *D. divergens* Imhof are quite frequent in the lakes, and we have also observed the var. *Schauinslandii* Lemm. of the latter species in Crummock (12. 7. 22). Its cells average $52\,\mu$ in length and have crenulations all along the margin. Moreover, they differ in not being "suddenly inflated below."

Interesting additions to previous records for this area are *Dinobryon stipitatum* Stein and *D. bavaricum* Imhof. Both are more delicate than *D. divergens* and have a stricter habit, the colonies being long, narrow, and very slightly branched. The cells are longer ($\pm\ 80\,\mu$), proportionally narrower and more gradually tapering below into long stipes. Pascher includes *D. bavaricum* under *D. stipitatum* as a sub-species and is probably justified in so doing. In *D. bavaricum* there is no marked basal inflation and the cell-margins have three or four crenulations in their widest part which is usually about the middle.

### Chlorophyceæ.

MOUGEOTIA ELEGANTULA Wittrock. West (Journ. Bot. vol. xxxvii.) gives the distribution of this species as Westmorland, West Ireland, and Sweden. We have collected it in Cumberland from Ennerdale, and it is especially abundant in Bassenthwaite. In Lancashire it occurs sparingly in Coniston and Esthwaite Water.

GONATOZYGON MONOTÆNIUM De Bary is commonly met with in all the lakes, but its rare variety, *pilosellum* Nordst., is found only in Hawes Water, Buttermere, and Windermere. West has recorded it from Hawes W. (Westmd.), but the present Cumberland and Lancashire records are additional.

GONATOZYGON KINAHANI (Arch.) Rabenh. is the only species of the genus with a perfectly smooth cell-wall. We have no previous records of it for the English lakes, but it occurs in the Cumberland lakes—Ennerdale, Buttermere, and Derwentwater—and also in Hawes W. (Westmd.).

GENICULARIA ELEGANS W. & G. S. West is a frequent constituent of the lake plankton, and is especially abundant in Ennerdale. West (Brit. Desm. i. 37) gives the following dimensions for this species :—Length 300–427 $\mu$, breadth 14–16·3 $\mu$, breadth of apices 17–18·5 $\mu$. We are of opinion that these figures need considerable revision. We have measured many Ennerdale specimens which were 200–217 $\mu$ in length by 14 $\mu$ broad with apices 17·5 or 18 μ across—a few were 186 × 13 μ, apices 14 μ. As *Gonatozygon monotænium* is frequently met with in the same collection, the question of dimensions assumes considerable importance. Especially is this the case when examining preserved material, in which the characteristic parietal and spirally twisted chloroplasts of *Genicularia elegans* may break down. West (*l. c.* 30) gives correctly for *Gonatozygon monotænium*, length 82–284 μ, breadth 7·5–11·5 μ, breadth of apices 8·6–12·5 μ. It would therefore appear from his measurements that the two species could be distinguished by their length alone. This, however, is by no means the case, as shown by the figures given above. We find, however, that the breadth of *Genicularia elegans* is invariably greater than that of *Gonatozygon monotænium*, and that, as a rule, the apical cell-wall is thicker, but we consider that the examination of fresh material is necessary for reliable determination.

SPIROTÆNIA TRABECULA A. Br. is an extremely rare desmid—previously unrecorded for England—which bears a superficial resemblance in size and shape to some forms of *Penium margaritaceum* (Ehrenb.) Bréb., but is readily distinguished by its cristate chloroplasts with their spiral ridges. One specimen only was observed in the Buttermere collection, 22 Sept., 1922.

PLEUROTÆNIUM CORONATUM (Bréb.) Rabenh., var. FLUCTUATUM West is another very rare form of which West gives no English records. It occurs, however, sparingly in four of our lakes and quite frequently in a fifth—Hawes Water—where we observed it in 75 per cent. of the samples taken. It differs from the normal form in having the lateral margins of the cell-walls undulate throughout their entire length. Forms intermediate between the type and the variety are occasionally met with. In these the lateral undulations are well marked in the lower half of the semi-cells, but gradually decrease in size in the upper part, often becoming obscure near the apex.

The genus MICRASTERIAS is well represented in the English lake plankton as our table shows. West (Brit. Desm. ii. 123) states that "in the British Islands *M. mahabuleshwarensis* var. *Wallichii* has only been found in the plankton of certain Scottish lochs." Its appearance, therefore, in eight of the eleven English lakes included in our survey seems to indicate a very rapid extension of its range of distribution, and also to suggest that it is a true plankton species. It is a specially prominent feature of the Bassenthwaite plankton and occurred in every sample examined. The great variation in form referred to by West (*l. c.*) is not apparent in the English specimens we have examined. As a rule they are remarkably uniform both in size and shape.

STAURASTRUM BRASILIENSE Nord., var. LUNDELLII West is an almost constant species in the plankton of Ennerdale and Derwentwater, and occurs also—sparingly—in Buttermere and Bassenthwaite. The original form from

Brazil was described by the author as being usually quadrangular in end view, and the angles as being often furnished with four spines. The Lake District forms are usually pentangular, and each angle has three spines.

S. OPHIURA Lund. is a conspicuous constituent of the Scottish and Welsh plankton, but is very rare in the English. In collections from Derwentwater, however, it is almost invariably present. In vertical view all the English specimens we have seen are eight-rayed.

West (in **5**) states that typical SPONDYLOSIUM PULCHRUM does not occur in the British Isles, but that Wolle's var. *planum* is quite common. This entirely agrees with our own experience, the variety being a ± constant constituent of the plankton of every English lake, and agreeing in size (lat. 12–25 $\mu$) with West's dimensions. We find also, in most lakes, a small form (lat. 7–10·5 $\mu$) which we have distinguished as f. *minor*. This has been observed frequently in Wa., En., Bu., Ba., Wi., and Es.

### Volvocales.

VOLVOX MONONÆ G. M. Smith is an interesting addition to the British phytoplankton species. It differs from *V. globator* and *V. aureus* in not having its cells connected by cytoplasmic processes. During late autumn it may form a prominent feature of the plankton of Hawes W., Windermere, and Esthwaite, often collecting as a visible surface-layer near the shores of Windermere in October or November.

### Heterokontæ.

CHLOROBOTRYS LIMNETICUS G. M. Smith is an addition to our British records of the Heterokontæ. It has been collected by us in three lakes and is most frequent in Ullswater.

### Bacillarieæ.

West recorded RHIZOSOLENIA MORSA for Wastwater, Ennerdale, and Windermere. It is still abundant in the last-named lake, but we have not yet seen it in the other two. It occurs also in Crummock, Derwentwater, and Esthwaite. Resting-spores were observed in specimens from Esthwaite (20.12.22), and in those from Derwentwater (a month earlier) were abundant.

### Myxophyceæ.

Although APHANIZOMENON FLOS-AQUÆ (L.) Ralfs has only been collected by us from one lake—Esthwaite—we have included it in our table on account of its exceptional abundance at certain seasons.

West's record of APHANOCAPSA DELICATISSIMA, having cells smaller than many bacteria (·5–·75 $\mu$ in diam.), is most interesting, but we have found *A. elachista* Naeg.—having cells ± 2 $\mu$—the more generally distributed plankton species in this lake area.

Another noteworthy addition is that of APHANOTHECE NIDULANS P. Richter in Hawes W. and Esthwaite. The var. *endophytica* West is endophytic in the sheaths of *Cœlosphærium Kutzingianum.*

ANABÆNA LEMMERMANNI P. Richter. Although this species occurred quite commonly in De., Ha., Wi., and Es., it was almost always collected as masses of spores. Less often it was found as small spherical masses consisting mainly of heterocysts, with a limited number of spores and a few very short vegetative cells. Very rarely it occurred as purely vegetative filaments with very few spores or heterocysts. On the other hand, *A. circinalis* was collected chiefly in the vegetative state. We are indebted to Professor F. E. Fritch for the identification of *A. Lemmermanni.*

## Peridinieæ.

West described PERIDINIUM WESTII Lemm. as a new British species from several Scottish lochs, in 1905. In our collection from Crummock W. (12. 7. 22) we observed it with some frequency—the first English record for this species.

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# Studies in the Phytoplankton of the Lowland Waters of Great Britain*. No. III. The Phytoplankton of Shropshire, Cheshire, and Staffordshire. By BENJAMIN MILLARD GRIFFITHS, D.Sc., F.L.S.

(PLATE 1.)

[Read 6th November, 1924.]

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SECTION 1. Topography of the area.

SECTION 2. Topography and phytoplankton of certain Shropshire Meres which exhibit the phenomena of water-bloom, and whose Myxophycean alga-flora was investigated by Wm. Phillips, F.L.S., in 1884.

SECTION 3. Topography and phytoplankton of waters other than the above.

SECTION 4. General account of the Alga-flora: species distribution, types of phytoplankton; Myxophyceæ, Bacillarieæ, Peridinieæ, Protococcales, Desmidieæ; distribution of organisms in the pool; general table of the Alga-flora.

## SECTION I.

THE area lying between the Potteries and the Welsh mountains and extending from Manchester to Shrewsbury might be described as the Lake District of the English Lowlands. It is a plain, seldom rising to a greater height than some four hundred feet, and it is drained by the rivers Dee, Weaver, and Severn. The rock is of Triassic age, but it is frequently covered with thick deposits of glacial gravels, especially towards the south. In ancient times there were great expanses of marsh and bog, and the higher ground was covered with forests, but the land is now drained and highly cultivated, and the only relic of the forests is Delamere Forest on the northern and eastern side. As in other parts of England, the land that could be drained was drained, but in this area are many pools which are situated in deep depressions in the glacial deposits, and their peculiar formation prevents them being drained by any ordinary means. These undrainable pools make the district practically unique in the English Lowlands; and though their areas seldom reach greater dimensions than one hundred and fifty acres and their depths as a rule do not exceed one hundred feet, they are nevertheless as truly natural bodies of water as the much more imposing lakes of the mountain areas. The most important group lies around Ellesmere, Salop, but other less-known groups exist north of Whitchurch, Salop, and a third in the neighbourhood of Knutsford, Cheshire. Of the pools on the Staffordshire borders, only the White Sitch at Weston-under-Lizard is natural, although the Great Pool at Patshull may have an ancient pool as its nucleus. Hammer Mere, Comber Mere, and the mere at Knutsford, although natural in origin, are also partly embanked, but Tabley Pool and Norton Mere are completely artificial.

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* Previous studies are:—I. The August Heleoplankton of North Worcestershire, Journ. Linn. Soc., Bot 1916; II. The Heleoplankton of three Berkshire Pools, Journ. Linn. Soc., Bot. 1922.

Most of the pools lie in the midst of park-land and pasture, and they are frequently bordered with trees. Marsh conditions are not extensive in these pools because of the general steepness of their banks. Bogs are rare, and never of any extent. The whole countryside is in a high state of cultivation —mainly pasture, as is the case in most of the Lowland regions,—and heathlands are absent. Owing to the elevation of the land the drainage is sluggish.

The bodies of water are variously called "pools" and "meres" irrespective of their origin or size. It is not possible to assign a strictly defined meaning to such terms as pond, pool, mere, or lake, but in the following discussion the term *pool* will be used as indicating any body of water less than about two hundred acres, and the term *lake* as indicating a body of water beyond that size.

As the pools are situated on the Trias or on the superposed glacial deposits, it might be assumed with considerable probability that the ratio of K and Na salts to Ca and Mg salts in their waters is low. In this respect they no doubt resemble the other waters of the great Eurasian Plain as developed in Denmark, Schleswig-Holstein, Finland, and Southern Sweden, and they differ from that of the western lakes of Britain and some of the Norwegian lakes which are situated on older and less calcareous geological formations. The pools are usually devoid of boggy margins, and in none is the water appreciably peaty.

## SECTION II.

In 1884, William Phillips, F.L.S., communicated to the Archæological and Natural History Society of Shropshire the results of his examination of the organisms which caused the discoloration or "breaking" of certain of the Shropshire meres (Phillips, **10**). His paper deals only with the Myxophyceæ, and nothing is said concerning other algæ, but the record is exceedingly valuable for determining any changes which may have taken place in the Myxophycean alga-flora during the thirty-eight years which have elapsed.

The Shropshire meres under consideration are all situated in the immediate vicinity of Ellesmere. They are all natural bodies of water, and are therefore of an age dating from the close of the Glacial Period. Geologically, the pools are kettle-holes or deep, steep-sided conical depressions in glacial gravels, and their water-supply is peculiar in that it is not derived from surface-streams but from the percolation of water through the gravelly strata. In many cases, too, the outflows are also by percolation. The pools tend to be rounded in outline and the banks slope down at a steep angle. They vary in area from about twenty to one hundred acres, but Kettle Mere is only five acres. They range in depth from about thirty to over seventy feet, and the deepest part is usually in the centre of the area.

In water-supply, size, depth, and shape these meres differ very markedly from the usually small, shallow and triangular artificial pools of the Lowlands. The topographical features result in an equally marked difference in the amount, distribution, and nature of the sediments, and of the macrophytic vegetation growing upon them, and the composition of the phytoplankton is different in consequence.

Owing to the absence of surface sources of water-supply, these meres do not receive contributions of water-borne sediment. Practically all their sediments are native, and are derived from the erosion of their own banks by wave action. The sediments which are formed in this way are partly laid down as a fringing band and partly carried out into deep water, and the latter transport is enhanced by the steep slope of the banks. The availability of the sediments for colonization by macrophytes is limited by the depth to which light will penetrate the water; and as the steep fall of the banks brings the photic limit close to the shore, the margins of the meres are characterized by very small and scanty weed-fringes. The only places in which vegetation can develop are in the few shallower bays which are found in some of the meres.

These meres therefore tend to be not only very self-contained, but very stable habitats. The normal geographical evolution associated with waters which are part of a surface drainage system does not occur; there are no inflowing surface streams gradually reducing the depth by the deposition of transported sedimentary matter, nor are there active outflowing streams which cut a deeper outflow channel and further reduce the depth and area. The scanty fringe of sediment does not encourage the growth of macrophytes, and those that are present cannot invade the water to any extent, because the floor of the basin slopes too rapidly below the photic limit.

Geographical development is therefore very slow, and it is quite possible that the meres present the same essential features as they did when first viewed by man. There must, however, be a change in the organic content of the water, firstly because the surrounding land has changed from forest to arable land, and the drainage water is therefore in all probability different, and secondly the photosynthetic activity of the macrophytes and the phytoplankton causes great quantities of carbon to be extracted from the carbon dioxide of the air and the water, and combined into carbon compounds as solid plant-substance. Some of this is no doubt lost on decay, but decay is not complete, and the residue remains as the richly organic deposits of mud around the edges of the pools.

DESCRIPTION OF THE POOLS AND THEIR PLANKTON CONTENTS, AUG. 1922.
(The name of the owner is given in parentheses.)

ELLESMERE LAKE (open to the public).—Area 115 acres; depth 65 feet. Surrounded by trees and parkland. Weed-fringe narrow and in patches, chiefly *Sparganium*, *Typha latifolia*, *Polygonum amphibium*, and some *Nuphar*. The old drainage channel ran through the town at a lower level than the present one. The bay between the island and the road was once covered with pine, and stumps have been removed recently from the bed of the lake at that point. There was a grey-green water-bloom.

Dominant: *Aphanizomenon Flos-aquæ*, many with gonidia; *Microcystis ochracea*. Sub-dominant: *Ceratium Hirundinella*, mostly with three basal horns, but some with only two; *Microcystis Flos-aquæ*; *M. æruginosa*; *Gomphosphæria Naegeliana*. Very rare: *Eudorina elegans*; *Staurastrum paradoxum* var. nov. *biradiatum*.

Phillips records *Rivularia articulata* Ag. = *R. echinulata* P. Richter from June to August 1883, and *Anabæna circinalis* in November 1883. (Phillips, **10**, p. 15.)

COLE MERE (Brownlow R. C. Tower, Esq., for Lord Brownlow).—Area 71 acres; depth 30 to 40 feet at northern end, but 9 or 10 feet in parts at south. Fairly continuous weed-fringe of *Arundo Phragmites* with occasional patches of *Scirpus lacustris* and *Typha latifolia* and in the bays a good deal of *Nymphæa alba*. Water a deep yellow-brown colour.

Dominant: *Ceratium Hirundinella,* mostly with two basal horns, but many with small third horn; many specimens showing early stage of cyst formation; *Asterionella formosa*. In smaller numbers: *Gomphosphæria Naegeliana*; *Fragilaria crotonensis*. Rare: *Coscinodiscus lacustris*; *Staurastrum paradoxum* var. nov. *biradiatum*; *Staurastrum paradoxum*; *Botryococcus Braunii*.

Phillips records *Aphanizomenon Flos-aquæ* in Aug. 1882. (**10**, p. 15.)

WHITE MERE (Brownlow R. C. Tower, Esq., for Lord Brownlow).—Area 64 acres; depth about 50 feet. Weed-fringe very small, but there are several bays containing *Nymphæa alba*, *Pol. amphibium*, *Typha*, and *Eleocharis*. Water a grey-green colour.

Dominant; *Anabæna affinis* var., gonidia attacked by a Chytrid fungus, but vegetative cells free from attack. Sub-dominant: *Ceratium Hirundinella*, with two basal horns; *Peridinium* sp.; *Gomphosphæria Naegeliana*; *Asterionella formosa*; *Melosira granulata*. In small numbers: *Fragilaria crotonensis*, *Staurastrum paradoxum* var. nov. *biradiatum*; *Coscinodiscus lacustris*. Rare: *Anabæna circinalis*; *Aphaniz. Flos-aquæ*; *Chroococcus limneticus*;

*Peridinium Willei*; *Staurastrum paradoxum*; *Pediastrum duplex*; *Eudorina elegans*; *Dictyosphærium pulchellum*. Very rare: *Rivularia echinulata*.

Phillips records *Anabæna circinalis*, July 1881 (p. 19).

NEWTON MERE (C. F. K. Mainwaring, Esq.).—Area 21 acres; depth 30 feet. Weed-fringe very scanty, consisting of a few patches of *Sparganium*, *Typha*, *Pol. amphibium*, and *Eleocharis*. For several years past the mere has been treated with copper sulphate to reduce the break. Water grey-green.

Dominant: *Microcystis æruginosa*. Sub-dominant: *Ceratium Hirundinella*, mostly with two basal horns, but small third in many, all horns shorter and thicker than usual: *Staurastrum paradoxum* var. nov. *biradiatum*. In smaller numbers: *Anabæna circinalis*; *Staurastrum gracile*; *Cosmarium reniforme*; *Tetracoccus botryoides*: *Eudorina elegans* attacked by a Chytrid. Rare: *Ped. duplex*; *Gomphosphæria Naegeliana*.

Phillips records *Dolichospermum Ralfsii* Kuetz. = *Anabæna affinis* var. in August 1881 (p. 18), but from Feb. to Aug. *Anabæna circinalis* and *Cœlosphærium Kuetzingianum*. He states that the "break" occurs several times in the year.

KETTLE MERE (C. F. K. Mainwaring, Esq.).—Area 4·5 acres; depth said to be very great. The mere is situated at the bottom of a deep conical depression, and communicates with Blake Mere by a shallow ditch. The grey-green water of Blake Mere was drifting through the ditch into Kettle Mere at the time of the examination. Water of Kettle Mere was opaque fawn colour. It is said to be contaminated by drainage. There is no weed-fringe, but there occur a few plants of *Nuphar* with unusually large leaves and fruits.

Dominant: *Aphanizomenon Flos-aquæ*, completely sterile. Sub-dominant: *Anabæna affinis* var., gonidia attacked by a Chytrid. Rare: *Microcystis Flos-aquæ*.

Phillips records *Anabæna circinalis* in July 1881 (p. 17).

BLAKE MERE (C. F. K. Mainwaring, Esq.).—Area 20 acres; depth about 40 feet in deep parts, but there are fairly extensive shallower bays supporting a vegetation of *Sparganium* and much *Nuphar*. Water grey-green.

Dominant: *Anabæna affinis* var., gonidia much attacked by Chytrid. Sub-dominant: *Ceratium Hirundinella*, mostly with two basal horns, but some with small third. Basal horns tend to lie at right angles to the girdle, and do not spread out as in more usual forms. In small numbers: *Anabæna circinalis*; *Eudorina elegans*; *Staur. paradoxum* var. nov. *biradiatum*.

The mere was never known to break until the last few years. The water was and still is reputed to be unusually soft (*see* Phillips, p. 17).

The following table shows the differences in the Myxophycean floras since 1884 :—

| | Ellesmere Lake. | | Cole Mere. | | White Mere. | | Newton Mere. | | Kettle Mere. | | Blake Mere. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| MYXOPHYCEÆ. | 1884 | 1922 | 1884 | 1922 | 1884 | 1922 | 1884 | 1922 | 1884 | 1922 | 1884 | 1922 |
| *Chroococcus limneticus* .... | .. | .. | .. | .. | .. | + | | | | | | |
| *Microcystis Flos-aquæ* .... | .. | + | | | | | | | | | | |
| ,, *ochracea* ...... | .. | + | | | | | | | | | | |
| ,, *æruginosa* ...... | .. | + | .. | .. | .. | .. | .. | + | | | | |
| *Gomphosphæria Naegeliana* .. | .. | + | .. | + | .. | + | .. | + | | | | |
| *Cœlosphærium Kuetzingianum* | .. | .. | .. | .. | .. | .. | + | | | | | |
| *Aphanizomenon Flos-aquæ* .. | .. | + | + | .. | .. | + | .. | .. | .. | + | | |
| *Dolichospermum Ralfsii*<br>*Anabæna affinis* var. } .. | .. | .. | .. | .. | .. | + | + | .. | .. | + | .. | + |
| ,, *circinalis* ........ | + | .. | .. | .. | + | + | + | .. | + | .. | .. | + |
| *Rivularia articulata*<br>,, *echinulata* } ...... | + | .. | .. | .. | .. | + | | | | | | |

It is evident that since 1884 there have been considerable changes in the flora. Of the five species recorded by Phillips, all were found in 1922 except *Cœlosphærium Kuetzingianum*, but their distribution is very different. As these algæ have definite periodicities, and as the latter do not necessarily occur exactly at the same time every season, no conclusions can be drawn from the results of a single collection.

## SECTION III.

Although the Ellesmere pools are very well known, they are not essentially different in structure from many others found in other parts of Shropshire and Cheshire. A number of pools will now be considered which are situated in various parts of the district extending from Shrewsbury to Manchester.

### The Albrighton group.

These pools lie on the borders of Staffordshire and Shropshire in the neighbourhood of the village of Albrighton.

CHILLINGTON POOL (W. T. C. Giffard, Esq., Chillington Hall, Staffs.).—Area 99 acres; depth about 30 feet near the dam. An artificial pool of considerable antiquity, lying amidst park and woodland, and running some distance northward as a long and narrow tongue. Several streams supply the pool, and in 1845, when the pool was drained, it took six months to refill. The shores are fringed with *Arundo* and some *Scirpus*.

Dominant: *Ceratium Hirundinella*, mixed two and three basal horns; *Volvox aureus*, *Anabæna circinalis*, *Glœocystis gigas*, *Sphærocystis Schroeteri*, in much divided state. In smaller number: *Microcystis æruginosa*, *Microcystis Flos-aquæ*. Rare: *Aphanizomenon Flos-aquæ*.

PATSHULL POOL (Earl of Dartmouth, Patshull Hall, Staffs.).—Area 62 acres; depth 40 feet in places. An artificial pool made by damming a valley. The upper part consists of two long and fairly shallow arms, but at the junction the water is deep. The pool lies in parkland. Weed-fringe of *Acorus Calamus*, *Typha angustifolia*, and some *T. latifolia*, *Scirpus*, *Arundo*, and fringing the shallower arms much *Nymphæa*, *Nuphar*, *Potamogeton natans*, and *Polygonum amphibium*.

Dominant: *Asterionella formosa*, *Gomphosphæria lacustris*; *Microcystis æruginosa*; *Gomphosphæria Naegeliana*, *Ceratium Hirundinella*, large three basal-horned form; *Dictyosphærium pulchellum*. Many: *Sphærocystis Schroeteri*, in much divided state; *Fragilaria crotonensis*: *Microcystis Flos-aquæ*; *Pediastrum duplex*. Few: *Staurastrum paradoxum* var. nov. *biradiatum*; *Eudorina*; *Cyclotella Kuetzingiana*; *Chroococcus lacustris*; *Anabæna circinalis*; *Pediastrum Boryanum*. Rare: *Anabæna affinis* var.

WHITE SITCH POOL (Earl of Bradford, Weston Park, Weston-under-Lizard).—Area 27 acres; depth about 10 feet along the north side, but for the larger part about 4 feet. The pool is natural and lies in the midst of an extensive wood. It is supplied by bottom springs and from the drainage of the wood. The bottom is gravelly. There is an extensive fringe of boggy marsh containing *Comarum palustre*, *Menyanthes trifoliata*, *Hypericum palustre*, *Ranunculus Lingua*, and on its edges are *Nymphæa*, *Pol. amphibium*, *Juncus* sp., a little *Typha latifolia*, and some amount of a small variety of *Scirpus lacustris* resembling *S. Tabernæmonti*. The bottom of the pool is covered with *Ceratophyllum*.

Abundant: *Xanthidium antilopeum*; *Ceratium Hirundinella*, with long apical horn and three rather short basal horns; *Ceratium cornutum*; *Pleurotænium Ehrenbergii*; *Closterium acicularis* var. *subpronum*; *Sphærozosma vertebratum*. Few: *Dictyosphærium pulchellum*; *Crucigenia rectangularis*; *Volvox aureus*; *Gomphosphæria Naegeliana*; *Peridinium bipes*; *Staurastrum furcigerum*; *Staurastrum Dickiei*; *St. brevispinum*; *Cosmarium Meneghinii*; *Pediastrum duplex*. Rare: *Sorastrum spinulosum*; *Cœlastrum sphæricum*; *Nephrocytium obesum*; *Glœocystis gigas*; *Asterionella formosa*; *Kirchneriella lunaris*.

WESTON PARK POOL (Earl of Bradford).—Area 12 acres; depth about 4 feet. An artificial pool lying in parkland. Bottom covered with

*Ceratophyllum* and *Myriophyllum.* Patches of *Acorus* and *Nymphæa* at the sides.

Dominant: *Microcystis æruginosa.* Rare: *Volvox aureus*; *Pediastrum duplex*; *Pandorina Morum*; *Xanthidium antilopeum.* Very rare: *Ceratium cornutum.*

NORTON MERE (Earl of Bradford).—Area 25 acres; depth from about 4 feet at the top end to 18 feet near the dam. An elongated artificial pool with a considerable stream running through. Parkland and plantations surrounding it. Extensive fringe of *Acorus* and *Nuphar* and patches of *Scirpus lacustris*, *Typha latifolia*, and *T. angustifolia.* Water greenish.

Dominant: *Anabæna affinis* var., very few gonidia, vegetable cells attacked by a Chytrid fungus; *Stephanodiscus* sp., *Asterionella formosa.* Few: *Pediastrum duplex*; *Eudorina*; *Scenedesmus quadricauda*; *Tetraedron minimum*; *Cœlastrum sphæricum*; *Pandorina Morum*; *Chodatella ciliata.*

### The Shrewsbury group.

ISLE POOL (Humphrey Sandford, Esq., The Isle, nr. Shrewsbury).—Area 14 acres; depth about 19 feet. The pool appears to be a kettle-hole, lying on the northern slope of a low hill of glacial gravel around which the River Severn runs in a loop. The bottom of the pool is well above the level of the river. In ancient times this extraordinarily situated pool was drained by a tunnel, and the present bottom was arable land. A century ago the tunnel fell in and the cavity filled with water to the brim, the water-area being about 27 acres. Later on, the pool was drained to the present level by means of a siphon. There is a nearly complete fringe of *Typha latifolia*, and there are considerable patches of *Nuphar* and *Nymphæa,* the latter water-lily being introduced about ten years ago. The pool "breaks" a brown colour, and the water was somewhat brown at the time of collection.

Dominant: *Dinobryon sertularia*; *Kirchneriella obesa.* Many: *Eudorina*; *Phacus longicauda* var. *torta*; *Aphanizomenon Flos-aquæ*; *Anabæna spiroides* var. *crassa.* Few: *Pediastrum Tetras*; *Tetraedron limneticum*; *Ceratium Hirundinella*; *Pediastrum duplex*; *Scenedesmus quadricauda,* with minute teeth (see West, **17**, p. 220, fig. E). Rare: *Tetrastrum staurogeniiforme*; *Peridinium anglicum*; *Staurastrum paradoxum* var. nov. *biradiatum.*

SHRAWARDINE POOL (William Everall, Esq., Shrawardine, Salop).—Area 35 acres; depth about 3 feet. The pool lies amidst pasture and parkland. It is artificial, but is apparently on the site of marshy land. The pool as it stands was constructed by the second Earl of Powis in the 18th century. It is fed entirely by springs. The bottom is sandy and there is a remarkable absence of bottom vegetation. This may be due to the presence of large numbers of wild-fowl. Fringing the sides are considerable patches of *Menyanthes* and some *Juncus.* The pool was considerably larger in past times. The collection could not be made very satisfactorily. The plankton was very scanty, consisting mainly of Copepods and Rotifers, together with *Pediastrum Boryanum*, *Pediastrum duplex*, and *Anabæna circinalis.*

### The Whitchurch, Salop, group.

In the neighbourhood of Whitchurch, Salop, on the borders of Shropshire and Cheshire, there occur a number of natural pools, some of which are scarcely inferior in size and depth to the better-known Ellesmere meres. Hanmer Mere lies between Ellesmere and Whitchurch, but the rest lie northward of the latter town.

HANMER MERE (Sir Edward Hanmer, Bettesfield Park, nr. Whitchurch, Salop).—Area 45 acres; depth said to be great in the centre, but there is a good deal of weed-fringe and wide reed-beds, consisting of *Typha angustifolia* with *Pol. amphibium* and *Nymphæa* in front. The mere has a natural nucleus, but the water-level has been raised a few feet by a small dam.

Dominant: *Asterionella formosa*; *Ceratium Hirundinella*, some with two and others with three basal horns; *Melosira granulata*; *Anabæna affinis* var.; *Eudorina*; *Dinobryon divergens*. Few: *Chroococcus limneticus*; *Dictyosphærium Ehrenbergianum*; *Peridinium Willei*; *Peridinium* sp. Rare: *Tetraedron limneticum*, form with four or five spines at the extremities of the furcated arms; *Microcystis æruginosa.*

MARBURY MERE (B. D. Poole, Esq., Marbury Hall, Whitchurch, Salop).—Area 25 acres; depth about 40 feet. The mere lies amidst pasture and parkland. There is a narrow and patchy fringe of *Arundo*, a little *Typha angustifolia* and *Scirpus lacustris*, and some *Nymphæa* and a lesser amount of *Nuphar*. The pool appears to be a kettle-hole, and the sides slope down with extreme steepness. The water was brown-green.

Dominant: *Ceratium Hirundinella*, mostly with two basal horns, but some with a very small third; a few encysted specimens were seen; *Aphanizomenon Flos-aquæ*; *Oscillatoria tenuis*. Few: *Closterium tortum*, sp. nov.; *Coscinodiscus lacustris*. Rare: *Asterionella formosa*; *Tetracoccus botryoides*; *Microcystis ochracea.*

COMBER MERE (Sir Kenneth Crossley, Combermere Abbey).—Area 146 acres; depth said to be 70 feet at one place, but the western end is much shallower. The nucleus of the pool is ancient, but the original level has been raised some six feet by a dam at the east end. The water is completely surrounded by parkland. There is a patchy fringing vegetation of *Arundo*, *Sparganium*, *Pol. amphibium*, *Nuphar*, and a little *Nymphæa*. Water dull grey in colour.

Dominant: *Aphanizomenon Flos-aquæ*. Sub-dominant: *Ceratium Hirundinella*, mostly two basal horns, but a few with a very small third. Rare: *Staurastrum paradoxum.*

OSS MERE (J. N. Joyce, Esq., Wicksted, Whitchurch, Salop).—Area 20 acres; depth about 12 feet at one end, but the other end is much shallower and the bottom has a considerable vegetation of *Potamogeton* and *Myriophyllum*. There is an almost continuous fringe of *Arundo* with many patches of *Nymphæa* in front. The pool is natural, and appears to be of the same origin as most of the previous ones. The water is surrounded by pasture and some plantations.

Dominant species did not occur, but there was an abundance of *Pediastrum duplex*, *P. Boryanum*; *Asterionella formosa*, with four rays; *Synedra berolinensis*; *Scenedesmus quadricauda*; *S. bijugatus*. Many: *Microcystis ochracea*; *Staurastrum paradoxum* var. nov. *biradiatum*. Few: *Gomphosphæria lacustris*; *Pediastrum biradiatum*; *Pediastrum tetras*; *Tetraedron minimum*; *Anabæna affinis* var.; *Ceratium Hirundinella*, with two basal horns; *Chroococcus limneticus*. Rare: *Eudorina*; *Cœlastrum sphæricum*; *Scenedemus obliquus*; *Selenastrum Bibraianum*.

BAR MERE (Marquis of Cholmondeley, Cholmondeley Castle).—Area 26 acres; depth not known, but supposed to be about 30 feet. The pool is rounded in outline, there is a narrow and almost continuous fringe of *Typha angustifolia* and some *Arundo*, with much *Nymphæa* and *Nuphar* in front. A small stream flows through. The water lies in the midst of pasture. The pool is natural and is apparently a kettle-hole.

Dominant: *Ceratium Hirundinella*, with two basal horns or with a small third horn; *Eudorina*. Many: *Mallomonas* sp. Few: *Coscinodiscus lacustris*; *Asterionella formosa*; *Fragillaria capucina*. Rare: *Pediastrum duplex*; *Tetracoccus botryoides*.

CHAPEL MERE (Marquis of Cholmondeley).—Area 24 acres; depth said to be considerable. There is a complete fringe of *Arundo* and *Typha angustifolia* and much *Nymphæa* and *Nuphar*. There are considerable areas of marshy ground around the pool. The water is entirely surrounded by park-land. The water-supply is from bottom springs, and drainage ditches connect the pool with the River Weaver.

The dominant organisms of the plankton were Rotifers, and the phytoplankton was not very abundant. Few: *Asterionella formosa*; *Ceratium Hirundinella*, mixed two and three basal horned forms; *Anabæna circinalis*; *Scenedesmus quadricauda*; *Crucigenia fenestrata*; *Crucigenia minima*; *Melosira granulata*, narrower form than in the other pools. Rare: *Pediastrum duplex*.

MOSS MERE (Marquis of Cholmondeley).—Area 24 acres; depth shallow at the north, but deepens south. There are fringing patches of *Arundo*, *Scirpus*, *Sparganium*, *Nymphæa*, *Nuphar*, and *Polygonum amphibium*. The water-supply is from bottom springs, the pool drains to Bar Mere. The water is surrounded by park-land, and there is a plantation at the south end.

Dominant: *Asterionella formosa*; *Ankistrodesmus falcatus* var. *mirabilis*. Rotifers were abundant, as in the neighbouring Chapel Mere. Many: *Pediastrum Boryanum*; *Gomphosphæria lacustris*; *Microcystis æruginosa*; *Anabæna Flos-aquæ*; *Ceratium Hirundinella*, small form with two basal horns. Few: *Gomphosphæria Naegeliana*; *Peridinium cinctum*; *Kirchneriella obesa*; *Chroococcus limneticus*. Very rare: *Anabæna affinis* var.; *Tetraedron regulare*.

### The Knutsford, Cheshire, group.

These pools lie in the neighbourhood of the town of Knutsford, on the northern edge of the district under consideration. Just to the south lies the salt-producing region of Cheshire, and northward is Manchester.

TABLEY POOL (C. Leicester-Warren, Esq., Tabley Hall).—Area 49 acres; depth about 12 feet in the centre, but only about 3 feet in the shallow arms. There are fringing patches of *Typha angustifolia* and *Arundo*, and the bottom is mostly covered with *Potamogeton pectinatus* and other pectinate-leaved species, but the shallow outlet arm has *Elodea*. There are bottom springs, but the pool is artificial and drains into the moat of Tabley Old Hall. Separate collections were made from the central weed-free area and from the shallow outlet arm.

The deep, weed-free central area contained:—Dominant: *Dinobryon Sertularia*; *Pediastrum duplex*. Many: *Fragilaria capucina*. Very rare: *Ceratium Hirundinella*, small form with two basal horns.

The shallow outlet arm contained:—Dominant: *Fragilaria capucina*. Many: *Cosmarium Botrytis*; *C. Turpinii*; *Dinobryon Sertularia*; *Closterium Leibleinii*. Rare: *Cosmarium biretum*; *Pediastrum duplex*.

THE MERE at Mere (David Isaacs, Esq., Mere New Hall).—Area 42 acres; depth said to be 100 feet in parts. Weed-fringe very scanty, mostly *Pol. amphibium* and *Nymphæa* and *Nuphar*. Water entirely surrounded with parkland. The pool is natural, but the level is raised a few feet by a dam. It drains to Rosthern Mere.

Dominant: *Ceratium Hirundinella*, mixed two and three basal horned; *Gomphosphæria Naegeliana*; *Microcystis Flos-aquæ*. Few: *Asterionella formosa*; *Staurastrum paradoxum*; *Microcystis æruginosa*. Rare: *Staurastrum paradoxum* var. nov. *biradiatum*; *Tetracoccus botryoides*; *Dictyosphærium pulchellum*; *Peridinium Willei*.

ROSTHERNE MERE (Lord Egerton of Tatton, Tatton Hall).—The topography of this lake has been fully described by Coward (Tattersall & Coward, **13**), and an account of the alga-flora as observed during 1922 and 1923 has been given by Pearsall (**9**).

The collection taken by the writer contained the following:—Dominant: *Fragilaria crotonensis*. Sub-dominant: *Gomphosphæria Naegeliana*;

*Closterium aciculare* var. *subpronum*. Many: *Ceratium Hirundinella*; *Staurastrum paradoxum*. Few: *Asterionella formosa*; *Staurastrum paradoxum* var. nov. *biradiatum*; *Eudorina*; *Microcystis Flos-aquæ*. Very rare: *Kirchneriella obesa*, *Peridinium Willei*.

## SECTION IV.

### *General account of the Plankton Alga-flora.*

The plankton alga-flora of this district comprised some eighty species, made up as follows:—

| Myxophyceæ. | Peridinieæ. | Bacillarieæ. | Protococcales. | Desmidieæ. |
|---|---|---|---|---|
| 13 | 7 | 8 | 31 | 18 |

The corresponding figures given by Messrs. West (**16**) for the phytoplankton of the larger lakes of Britain and Ireland are

| | | | | |
|---|---|---|---|---|
| 53 | 15 | 94 | 65 | 236 |

A comparison of these figures shows that the district contains only about one-sixth of the number of species recorded by Messrs. West*, and that proportionately the district has more Myxophyceæ and Peridinieæ and a much larger proportion of Protococcales, but that it is relatively poor in Bacillarieæ and Desmids.

There is a resemblance, in fact, rather to the lakes of the Continent than to the somewhat exceptional lakes of the British mountain areas, upon which so many of Messrs. West's observations were made. The resemblance to Continental lakes has already been pointed out by the writer (Griffiths, **5**, p. 205), and Pearsall comes to the same conclusion in reference to Rostherne Mere (Pearsall, **9**, p. 55). The western mountain lakes are on rocky areas of great geological age, and their water-supply is much less rich in calcium salts and organic matter than is the case either in the English lowlands or in the rest of the great European plain. Their plankton is characterized by great numbers of species of desmids, but the bulk of the plankton is small, and water-blooms are rare or absent. In the pools of this district the waters are relatively rich in dissolved salts and organic matter, very few desmids occur, and though the number of algal species is not great, some of them attain an enormous abundance, causing marked discoloration of the water, the causative organisms being chiefly Myxophyceæ, *Ceratium Hirundinella*, and occasionally *Dinobryon*. This amazing profusion is not universal in the pools of the district, but tends to be restricted to waters of a certain depth and volume, and the less deep pools tend to have more species, but not a superabundance of any one of them.

In the following table the pools are arranged according to the dominance or sub-dominance of Myxophyceæ, Peridinieæ, Bacillarieæ, Protococcales, and

---

* As the figures are based on a single late summer collection from each pool, the actual number of species is not strictly comparable with Messrs. West's list. Collections throughout the year would probably show a much more extensive flora.

Desmidieæ in their waters. Even on this basis of a single late summer collection, the pools fall into a series which tends to coincide with their variations in size and depth. In the first group of pools, Myxophyceæ, Peridinieæ, and Bacillarieæ tend to be dominant, but Protococcales are subsidiary or absent. Physically, these pools are characterized by great volume or depth of water, resulting in the possibility of stagnation layers,

TABLE showing the number of species found in each pool. Abundant species are shown in italic figures

| | MYXOPHYCEÆ. | PERIDINIEÆ. | BACILLARIEÆ. | PROTOCOCCALES. | DESMIDIEÆ. | Others. | Total No. of Species. |
|---|---|---|---|---|---|---|---|
| 1. Ellesmere Lake . . | *5* | *1* | . . | 1 | 1 | . . | 8 |
| 2. Newton Mere. . . . | *1.* 2 | *1* | . . | 3 | 3 | . . | 10 |
| 3. Blake Mere . . . . | *1.* 1 | *1* | . . | 1 | 1 | . . | 5 |
| 4. Mere, Knutsford . | *2.* 1 | *1.* 1 | 1 | 2 | 2 | . . | 10 |
| 5. Marbury Mere . . | *2.* 1 | *1* | 2 | 1 | 1 | . | 8 |
| 6. Comber Mere. . . . | *1* | *1* | . . | . . | 1 | . . | 3 |
| 7. Kettle Mere . . . . | *1.* 3 | . . | . . | . . | . . | . . | 4 |
| 8. Rostherne Mere . . | *1.* 2 | 1 | *1.* 1 | 2 | *1.* 2 | . . | 11 |
| 9. Cole Mere . . . . . . | 1 | *1* | *1.* 2 | 1 | 1 | . . | 7 |
| 10. Hanmer Mere . . | *1.* 2 | *1.* 2 | *2* | *1.* 2 | . . | 1 | 12 |
| 11. Bar Mere . . . . . . | . . | *1* | 3 | *1.* 2 | . . | *1* | 8 |
| 12. White Mere . . . . | *2.* 4 | *2.* 1 | *2.* 2 | 3 | 2 | . . | 18 |
| 13 Patshull Pool. . . . | *3.* 4 | *1* | *1.* 2 | *1.* 4 | 1 | . . | 14 |
| 14. Chillington Pool . | *1.* 3 | *1* | . . | *3* | . . | . . | 8 |
| 15. Oss Mere . . . . . . | 5 | 1 | *2* | *4.* 6 | 1 | . . | 19 |
| 16. Chapel Mere . . . . | 1 | 1 | 2 | 4 | . . | . . | 8 |
| 17. Moss Mere . . . . . . | 6 | 2 | *1* | *1.* 3 | . . | . . | 13 |
| 18. Norton Mere . . . . | *1* | . . | *2* | 7 | . . | . . | 10 |
| 19. Isle Pool. . . . . . . . | 4 | 2 | . . | *1.* 6 | 1 | *1.* 1 | 16 |
| 20. White Sitch . . . . | 1 | *2.* 1 | 1 | 9 | *4.* 5 | . . | 23 |
| 21. Tabley Pool . . . . | . . | 1 | 1 | *1* | 4 | *1* | 8 |
| 22. Weston Park . . . . | *1* | 1 | . . | 3 | 1 | . . | 6 |
| 23. Shrawardine Pool. | 1 | 1 | . . | 1 | . . | . . | 3 |

sediments lying in oxygen-poor regions and the limitation of the submerged macrophytic vegetation to narrrow marginal fringes. The alga-flora is "limnoplanktonic" in type.

At the other end of the series, Myxophyceæ, Peridinieæ, and Bacillarieæ tend to diminish, and Protococcales are dominant. These pools are apt to become less deep, so that the whole volume of water tends to be kept in circulation by the wind, and the penetration of the light allows greater growth of macrophytic vegetation upon the sediments. The alga-flora is "benthoplanktonic" in type.

The intermediate pools show a transition from one type to the other, and representatives of all classes occur. Physically these pools are either deep in one part and shallow in another, *e. g.* Oss Mere, or the main basin is deep, but there is a shallow rim, *e. g.* Hanmer Mere, and to some extent even White Mere, or there is a flow of water through the pool, *e.g.* Norton Mere and perhaps Bar Mere. The alga-flora is "heleoplanktonic" in type (see Griffiths, **5**, p. 209).

Completely benthoplanktonic floras, such as those encountered in the smaller and shallower artificial pools of the Midlands and elsewhere in the lowlands, are not typically developed in the district, except in so far as the heleoplanktonic type is intermediate between bentho- and limnoplankton.

## THE DESMIDIEÆ.

"Desmid plankton" in the sense used by Messrs. West (**16**, p. 196) does not occur in the pools of this district. Desmids form only a very subsidiary part of the plankton in most cases, but nevertheless certain species are quite characteristic.

The most typical desmid is a biradiate form of *Staurastrum paradoxum* Meyen (Pl. **1**. figs. I, II, III). It was found in the greater number of the larger pools, and occurred in quite considerable abundance in Newton Mere. It was frequently associated with the type-form, and in one instance with *St. gracile* Ralfs, the association being as follows :—

| | |
|---|---|
| *Staur. paradoxum* var. nov. *biradiatum* | 1. 2. 3. 4. 8. 9. 12. 13. 15. 19. |
| ,, ,, Meyen, type-form ... | 4. 6. 8. 9. 12. |
| ,, *gracile* Ralfs .................... | 2. |

(Numerals refer to index number of pools in Table, p. 87.)

A biradiate form of *Staur. paradoxum* Meyen is briefly mentioned and figured by Dr. Nellie Carter from the ancient Bracebridge Pool, Sutton Park, Warwickshire (West & Carter, **18**, p. 103, pl. 145. fig. 5). The form occurring in this district differs from the above in being considerably larger, its processes longer and more slender and more widely spread, and the isthmus relatively narrower. In some respects the form tends rather towards the plankton variety *longipes* Nordst., but it is smaller and has a narrower isthmus, besides being biradiate. It is very much larger than *Staur. tetracerum,* besides differing in detail.

Comparative measurements of the above forms are summarized below :—

| | Length of cell. | Width across processes. | Width of isthmus. |
|---|---|---|---|
| *St. paradoxum* Meyen .................... | 21–36 μ | 41–70 μ | 5–12 μ |
| ,, ,, biradiate form of West & Carter. | 19·5 | 55 | 7·8 |
| ,, ,, var. *longipes* Nordst. ........ | 26–29 | 84–139 | 8·0–9·5 |
| ,, ,, var. nov. *biradiatum*.......... | 20–30 | 55–70 | 4–5 |
| ,, *tetracerum* Ralfs ..................... | 7–10 | 18 30 | 4–8 |

It will be noticed that the pools in which *St. paradoxum, St. gracile,* and *St. paradoxum* var. *biradiatum* occur tend to be of the limno- and heleo-planktonic type. The two former species are common in the lakes of the Continent (Wesenberg-Lund, **14**, p. 423), but are not characteristic of the desmid planktons of the western mountain lakes. It might also be mentioned that *St. paradoxum* var. *biradiatum* was found by the writer in some of the pools of Anglesey in the summer of 1923. The desmid appears to be characteristic of the natural lowland pools of this district, and it is therefore described as a definite variety :—

STAURASTRUM PARADOXUM Meyen, var. nov. BIRADIATUM.

Semicellulæ duobus gracilibus processis ornatæ. Long. cell. 20–30 μ ; lat. proc. 55–70 μ ; crass. isthm. 4–5 μ. In plankton lacuum Shropshire, Cheshire (et Insula Anglesey).

In Marbury Mere there occurred a species of *Closterium* which appears to differ from previously recorded species, especially in the remarkable torsion of the cell (Pl. **1**. figs. IV, V, VI). The middle region of the cell lies in one plane as in other species, but the apical regions are curved sharply in a direction transverse to the median plane. Sometimes one apex only is curved, but in other cases one apex is curved towards the right and the other towards the left. The general result is to give the whole cell a semi-helicoidal torsion. The desmid differs from *C. Cornu* Ehrenb. in having distinctly pointed and not rounded apices, and in being twisted so markedly, but it agrees more or less in size, in number of pyrenoids, and in having one granule in the terminal vacuole. It differs from *C. Ceratium* Perty in being rather stouter, much more twisted, and in being devoid of the acicular apices. Comparative measurements are as follows :—

| | Length across apices. | Breadth. | No. pyrenoids. | No. granules. |
|---|---|---|---|---|
| *C. Cornu* Ehrenb. | 110–165 μ | 6·5–8·8 μ | 3–5 | 1 |
| *C. Ceratium* Perty | 110–260 | 6·0–6·5 | 4–5 | 1 |
| *C. tortum*, sp. nov. | 90–100 | 8–10 | 3–4 | 1 |

The desmid was only found in Marbury Mere. It was associated with limnoplanktonic species such as *Ceratium Hirundinella*, *Asterionella*, *Aphanizomenon*, and *Coscinodiscus lacustris.* The pool has sides of such steepness that ducks cannot be kept upon it because of the absence of sufficient mud-fringe with submerged aquatic vegetation. It might be suggested that the alga is a local species derived from some form like *C. Cornu*, whose tendency to develop torsion may have had survival value in this limnetic habitat. (Compare the spirally coiled variety of *Mougeotia* described by West & West, **16**, p. 169.)

CLOSTERIUM TORTUM, sp. nov.

Cellula parva, torta semi-helicoidaliter ; apices acutiformes sed rotundati ; pyrenoides 3–4 ; unus granulus in vacuolo terminali. Long. 90–100 μ ; crass. 8–10 μ. In plankton Marbury Mere juxta Whitchurch, Shropshire.

*Closterium aciculare* var. *subpronum* West & West occurred abundantly in Rostherne Mere and in the White Sitch, two rather different habitats. The desmid has been recorded previously as a dominant in Bulmershe South Pool, Reading (Griffiths, **4**, p. 6). It is commonly found in the lakes of Sweden, but not usually in great abundance (Borge, **1**, p. 14), and it is also recorded for Lough Neagh, a British lake of the Continental type (West & West, **16**, p. 177).

Most of the other desmids recorded for the district occurred in the White Sitch and in Tabley Pool, both of which have a considerable submerged macrophytic flora. In the case of Tabley Pool, the desmids were only found in the shallow arm, and did not occur over the deepest part.

## THE MYXOPHYCEÆ.

Conspicuous developments of Myxophyceæ were found in many of the larger pools, but less frequently in the smaller. The algæ responsible for the water-blooms were chiefly :—*Gomphosphæria Naegeliana*, in five pools ; *Aphanizomenon Flos-aquæ* in four ; *Microcystis æruginosa* in four ; *Anabæna* *affinis* var. in three; *Microcystis Flos-aquæ* in two; *Microcystis ochracea* and *Oscillatoria tenuis* in one. Frequently several occurred together, and no less than five species made up the water-bloom of Ellesmere Lake. *Cœlosphærium Kuetzingianum* was not found; it appears to be a late autumnal and spring form in Rostherne Mére (Pearsall, **9**, table p. 54), and Phillips records it for Newton Mere in 1881 as appearing from February to August (Phillips, **10**, p. 18).

The most interesting of the above species is the variety of *Anabæna affinis* Lemm., which was found in the pools of the Albrighton, Ellesmere, and Whitchurch groups, but not in the Knutsford group farther north. The alga is described and figured by Phillips as *Dolichospermum Ralfsii* Kuetz. (Phillips, **10**, p. 22, fig. 4 of plate). It differs from *A. affinis* only in size, the vegetative cells being considerably wider, and from *A. limnetica* G. M. Smith (Smith, G. M., **12**, p. 57, pl. 8. fig. 8) in being smaller. In size it resembles *A. affinis* var. *holsatica* Lemm. (Lemmermann, **7**, p. 183) and *A. planctonica* Brunnthaler (Smith, G. M., **12**, p. 56, pl. 8. fig. 2), but differs from the former in the shape of the heterocyst, and from the latter in the shape of the spore. There is a wide and delicate sheath, invisible in water, but readily demonstrated by the Indian-ink method (see Pl. **1**. fig. VIII). Its relationship to the above algæ is shown in the following table:—

| | Vegetative Cell. | Heterocyst. | Spore. | |
|---|---|---|---|---|
| | | | Breadth. | Length. |
| *A. affinis* Lemm. (acc. to Lemmermann) | ca. 7 μ | 7·5–8·0 μ | 9·5–12·0 μ | 20–26 μ |
| *A. affinis* Lemm. (acc. to G. M. Smith) | 5–6 | 7·5–10·0 | 9·5–12·0 | 17–26 |
| *A. affinis* var. *holsatica* Lemm. | 9–11 | 4·5–11 by 10–13 | 11–13 | 22–29 |
| *A. planctonica* Brunnth. (acc. to G. M. Smith) | 9–15 | 12–14 | 12·5–20 | 12·5–30 |
| *A. limnetica* G. M. Smith | 12–15 | 10–14 | 17–20 | 20–30 |
| *A. affinis* var. nov. *intermedia* | 8–10 | 8–10 | 12–16 | 17–26 |

The alga appears, therefore, to be a variant of *A. affinis*, intermediate in size between it and *A. limnetica* G. M. Smith.

*Anabæna affinis* is not mentioned in Messrs. West's list of the British plankton algæ (West & West, **16**, p. 187), nor is it given in Grove's list of algæ in the Birmingham district. It is apparently by no means rare in Continental lakes, and even causes water-blooms (see Lemmermann, 7, p. 183). G. M. Smith describes it as occurring with *A. planctonica* and *A. limnetica* in American waters. The occurrence of the alga in the Shropshire and southern Cheshire waters tends, therefore, to link these pools with those of the Continent and N. America rather than with the western mountain lakes. (The alga was also found by the writer in some of the lakes of Anglesey in the summer of 1923.)

Diagnosis:—ANABÆNA AFFINIS Lemmermann, var. nov. INTERMEDIA. Similis exemplo sed major. Cell. veg. lat. 8–10 $\mu$; heterocystis 8–10 $\mu$; sporis, lat. 12–16 $\mu$, long. 17–26 $\mu$. In lacubus Shropshire, Cheshire (et Insula Anglesey), England.

## The Bacillarieæ.

Much the most prominent diatom in the deeper pools is *Asterionella formosa,* but it is seldom found in any abundance in the shallower ones. The number of cells per colony is variable. Messrs. West (**15**, p. 514) state that in the Scottish and other western British lakes the number of cells per colony is usually eight, though seven and nine also occur, but that Continental authors frequently record three, four, or five cells per colony. The following table gives the number of cells per colony observed in the pools of this district:—

| | | | |
|---|---|---|---|
| The Mere, Knutsford…… | 12 | Patshull Pool ………… | 8 |
| Rostherne Mere ………… | 12 | Oss Mere ……………… | 4 |
| Cole Mere ……………… | 8 | Chapel Mere ………… | 4 |
| Hanmer Mere…………… | 8 | Moss Mere …………… | 8 |
| Bar Mere ……………… | 8 | Norton Mere…………… | 5, 8 |
| White Mere …………… | 8 | | |

It will be noted that the limnoplanktonic pools tend to have a number in agreement with that of the deep lakes, but that the heleoplanktonic pools have lesser numbers. The benthoplanktonic pools are, as a rule, devoid of *Asterionella.*

*Melosira granulata* occurred in White Mere, Hanmer Mere, and Chapel Mere. The diatom is a typical constituent of the plankton of the Continental lakes, and also occurs regularly in some of the British lakes, though not in such abundance. It is unusual in the lowland pools, and occurs only in those which approach the size of lakes.

*Coscinodiscus lacustris* occurred in Cole Mere, White Mere, Bar Mere, and Marbury Mere. It is recorded for the plankton of Lough Neagh, Ireland (West & West, **16**, p. 185). It is very rare in the smaller pools.

*Fragilaria crotonensis* formed the dominant alga of Rostherne Mere, and also occurred in White Mere, Cole Mere, and Patshull Pool. It is characteristic of the larger lakes (West & West, **16**, p. 513) of both Britain and the Continent (Schoenfeldt, **11**, p. 34).

A notable point about the diatom flora of the lowland pools is the practically complete absence of *Tabellaria.* This diatom is characteristic of many of the western mountain lakes, and often occurs as a dominant. It might be pointed out that the above lakes are very frequently peaty, but that these lowland lakes are seldom so. (See also Griffiths, **5**, p. 206.)

## THE PERIDINIEÆ.

*Ceratium Hirundinella* is much the most abundant Peridinian of the pools of this district and of the lowland pools in general. It occurs frequently in association with *Asterionella*. It does not occur in abundance in the smaller and shallower pools, nor in pools of the riverine type, but appears to require relatively deep-water conditions. Although of unmistakable shape, it is extraordinarily variable in detail, and also varies considerably in size. The most prevalent form in these pools has two basal horns, but forms with three basal horns, the third being of very variable size, frequently occur plentifully along with the former. Variation of form in the same body of water is frequent in lakes (Lemmermann, **7**, p. 647), but in pools the tendency appears to be towards greater constancy (Griffiths, **4**; also Lemmermann, **7**, p. 647).

Abnormalities in morphology were not exceedingly rare. They included cases of branching of apical and basal horns, and a kind of twinning in which the normal fission of the organism had stopped before completion, so that the resulting couple of cells were united more or less completely. A number of cases were observed in which there was an apparent conjugation, but these appearances are probably due to the fact that at the moment of death the alga very frequently eviscerates itself via the longitudinal furrow, and in the densely crowded collecting-tube accidental adherence of freshly-protruded protoplasts might easily take place (see also remarks of Oltmanns, **8**, p. 68). Cyst formation was observed in Cole Mere, where it was very frequent. It was also seen, though more rarely, in Marbury Mere and Blake Mere.

*Ceratium cornutum* is a rare alga in the lowland pools, but it is found in quantity in some of the larger lakes, particularly in Wales (West & West, **16**, p. 173). The alga occurred in considerable numbers in the White Sitch, Weston-under-Lizard, and very rarely in Weston Park Pool, not very far away. The writer has also observed it in a pool in the limestone of Benthall Edge, near Ironbridge, Shropshire, and Hodgetts records it from a small pool near Birmingham (Grove, etc., **6**, p. 10).

*Peridinium cinctum*, *P. Willei*, and *P. bipes* were not found in any abundance in either the deep or the shallow pools of this district. All are frequently abundant in lakes, but the only cases of dominance in the lowland pools known to the writer are those of the two Bulmershe Pools near Reading, and in Rothley Lake, Northumberland, and in Ryton Willows Pool, Newcastle-on-Tyne.

## THE PROTOCOCCALES.

The Protococcales constitute nearly 50 per cent. of the phytoplankton species, and considerably outnumber any of the other groups. In the deepest and largest pools they are represented only by a few species which are peculiar to limnoplanktonic conditions, e. g. *Tetracoccus botryoides.* They are most freely developed in the shallower pools, but no case was observed in which Protococcales were responsible for water-bloom. Dominance of any one species seldom occurred, but in many instances several species occurred in considerable abundance in the same pool, *e.g.* Oss Mere with ten, the White Sitch with nine, and Norton Mere and Isle Pool with seven species.

*Pediastrum duplex* Meyen occurred in eleven pools; it appears to be heleoplanktonic rather than limnoplanktonic in type. *Eudorina elegans* Ehrenb. also occurred in eleven pools, but it ranges rather more towards the limnetic end of the scale than *P. duplex.*

Certain rare Protococcales were found:—

*Crucigenia fenestrata* Schmidle occurred in fair numbers in Chapel Mere, Cholmondeley, Cheshire. It appears to be a new record for this country. Brunnthaler (**2**, p. 173, fig. 252) records it from Breslau and Italy*.

*Crucigenia minima* (Fitschen) Brunnthaler (**2**, p. 174) also occurred in some quantity in the same pool. It had previously been found in Whiteknights Pool, Reading (Griffiths, **4**, p. 10).

*Tetrastrum staurogeniiforme* (Schroeder) Chodat was found in the Isle Pool, near Shrewsbury. It was previously known from Spring Grove Upper Pool, near Kidderminster (Griffiths, **3**, p. 431).

*Sorastrum spinulosum* Naegeli (see Pl. **1**. fig. VII) occurred as a very rare alga in the White Sitch. It resembles the typical form in having a very small central sphere, but the cell-form approaches that of *S. spinulosum* var. *hathoris* (Cohn) Schmidle and *S. americanum* (Bohlin) Schmidle (see Brunnthaler, **2**, p. 201). The last is recorded for a pool in the Outer Hebrides by West (**17**, p. 215), and differs from the White Sitch specimen in having a very conspicuous central sphere.

## THE DISTRIBUTION OF ORGANISMS IN THE POOL.

All the plankton collections were taken as nearly as possible over the deepest water in the centre or middle of the pool, and only one collection was made as a rule. Investigations on certain pools in Northumberland have shown that in some of these smaller bodies of water the plankton is by no means uniformly distributed over the surface of the water (Griffiths, **5**,

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* Brunnthaler's fig. 252 is reproduced in Oltmanns **8**, vol. i. p. 271, fig. 182, but is apparently erroneously named "*C. Tetrapedia.*"

p. 196, etc.). During the present investigation a regional examination was made of Tabley Pool, Knutsford, Cheshire, one collection being taken over the part which was deep and free from weeds, and a second from the shallow northern arm of the pool. The two collections were visibly different, that from the deep area being a yellow-brown colour, and that from the shallow water not brown. The plankton over the deep water consisted of *Dinobryon* in great abundance, together with *Pediastrum duplex*, many *Fragilaria capucina* and rare *Ceratium Hirundinella*. That over the shallow water comprised very few *Dinobryon* or *Pediastrum duplex*, but *Fragilaria* in great abundance, together with great numbers of Desmids of shallow-water type.

It is probable that in pools with a small volume of water and variable depth these variations in distribution are normal. In the large lake the plankton is probably much more uniform, though perhaps the shallower bays might yield a different plankton flora.

## THE ALGA-FLORA.

(After each species are placed the serial numbers of the pools in which the species occur. Abundant occurrence is indicated by italic figures.)

### MYXOPHYCEÆ.

*Anabæna circinalis* (Kuetz.) Hansg. 2. 3. 7. 12. 13. *14*. 16. 23.
,, *Flos-aquæ* (Lyngb.) Bréb. 17.
,, *affinis* Lemm., var. *intermedia*. 3. 7. *10. 12*. 13. 15. 17. *18*.
,, *spiroides* var. *crassa* Lemm. 19.
*Oscillatoria tenuis* Ag. *5*.
*Rivularia echinulata* P. Richter. 12.
*Gomphosphæria Naegeliana* (Unger) Lemm. *1*. 2. *4. 8*. 9. *12. 13*. 17. 19. 20.
,, *lacustris* Chodat. *13*. 15. 17.
*Microcystis æruginosa* Kuetz. *1. 2. 4*. 10. *13*. 14. 17. 22.
,, *Flos-aquæ* (Wittr.) Kirch. *1. 4*. 7. 8. 13. 14. 19.
,, *ochracea* (Brand) Forti. *1*. 5. 15.
*Chroococcus limneticus* Lemm. 10. 12. 13. 15. 17.
*Aphanizomenon Flos-aquæ* (L.) Ralfs. *1. 5. 6. 7*. 12. 14. 19.

### PERIDINIEÆ.

*Ceratium cornutum* (Ehrenb.) Cl. & Lach. *20*. 22.
,, *Hirundinella* O. F. Mueller. *1. 2. 3. 4. 5. 6*. 8. *9. 10. 11. 12. 13. 14*. 15. 16. 17. 19. *20*. 21.
*Perdinium bipes* Stein. 20. 23.
,, *Willei* H. Kass. 4. 8. 10. 12.
,, *cinctum* Ehrenb. 17.
,, *anglicum* G. S. West. 19.
,, sp. 10. 12.

### BACILLARIEÆ.

*Melosira granulata* (Ehrenb.) Ralfs. *10. 12*. 16.
*Cyclotella Kuetzingiana* Chauvin. 13.
*Coscinodiscus lacustris* Grun. 5. 9. 11. 12.
*Stephanodiscus* sp. *18*.

*Fragilaria crotonensis* (A. M. Ed.) Kitton. *8.* 9. 12. 13.
,, *capucina* Desmaz. 11. 21.
*Asterionella formosa* Hass. 4. 5. 8. *9. 10.* 11. *12. 13. 15.* 16. *17. 18.* 20.
*Synedra berolinensis* Lemm. *15.*

### Protococcales.

*Volvox aureus* Ehrenb. *14.* 20. 22.
*Eudorina elegans* Ehrenb. 1 2. 3. 8. *10. 11.* 12. 13. 15. 18. 19.
*Pandorina Morum* (Muell.) Bory. 18. 22.
*Pediastrum Boryanum* (Turp.) Menegh. 13. *15.* 17. 23.
,, *duplex* Meyen. 2. 11. 12. 13. *15.* 16. 18. 19. 20. *21.* 22.
,, *biradiatum* Meyen, var. *emarginatum* A. Braun. 15.
,, *tetras* (Ehrenb.) Ralfs. 15. 19.
*Sorastrum spinulosum* Naeg. var. 20.
*Cœlastrum sphæricum* Naeg. 15. 18. 20.
*Crucigenia rectangularis* (Naeg.) Gay. 20.
,, *fenestrata* Schmidle. 16.
,, *minima* (Fitschen) Brunnth. 16.
*Scenedesmus bijugatus* (Turp.) Kuetz. *15.*
,, *obliquus* Kuetz. 15.
,, *quadricauda* (Turp.) Bréb. *15.* 16. 18. 19.
*Ankistrodesmus falcatus* (Corda) Ralfs, var. *mirabilis* G. S. West. *17.*
*Selenastrum Bibraianum* Reinsch. 15.
*Kirchneriella lunaris* (Kirsch.) Moeb. 20.
,, *obesa* W. & G. S. West. 8. *19.*
*Nephrocytium obesum* West. 17. 20.
*Tetraedron minimum* Hansg. 15. 18.
,, *regulare* Kuetz. 17.
,, *limneticum* Borge. 10. 19.
*Dictyosphærium pulchellum* Wood. 4. 12. *13.* 20.
,, *Ehrenbergianum* Naeg. 10.
*Botryococcus Braunii* Kuetz. 9.
*Sphærocystis Schroeteri* Chodat. 13. *14.*
*Glœocystis gigas* (Kuetz.) Lagerh. *14.* 20.
*Tetracoccus botryoides* W. West. 2. 4. 5. 11.
*Tetrastrum staurogeniiforme* (Schroeder) Lemm. 19.
*Chodatella ciliata* (Lagerh.) Lemm. 18.

### Desmidieæ.

*Closterium aciculare* var. *subpronum* W. & G. S. West. *8. 20.*
,, *Leibleinii* Kuetz. 21.
,, *tortum*, sp. nov. 5.
*Pleurotænium Ehrenbergii* (Ralfs) De Bary. *20.*
*Cosmarium Botrytis* Menegh. 21.
,, *biretum* Bréb. 21.
,, *Turpinii* Bréb. 21.
,, *Meneghinii* Bréb. 21.
,, *reniforme* (Ralfs) Archer. 2.
*Xanthidium antilopeum* (Bréb.) Kuetz. *20.* 22.
*Staurastrum brevispinum* Bréb. 20.
,, *Dickiei* Ralfs. 20.
,, *furcigerum* Bréb. 20.

*Staurastrum gracile* Ralfs. 2.
„ *paradoxum* Meyen. 4. 6. 8. 9. 12.
„ „ var. *biradiatum* var. nov. 1. 2. 3. 4. 8. 9. 12. 13. 15. 19.
*Sphærozosma vertebratum* Ralfs. *20.*
*Desmidium Swartzii* Ag. 20.

*Dinobryon Sertularia* Ehrenb. *19. 21.*
„ *divergens* Imhof. 10.
*Phacus longicauda* var. *torta* Lemm. 19.
*Mallomonas.* 11.

Total of species:—

| | |
|---|---|
| Myxophyceæ | 13 |
| Peridinieæ | 7 |
| Bacillarieæ | 8 |
| Protococcales | 31 |
| Desmidieæ | 18 |
| Others | 4 |
| | 81 |

In concluding this account of the plankton of the pools of Shropshire, Staffordshire, and Cheshire, I wish to express my thanks to the owners of the pools for their kind permission to take collections, and for the assistance and information they have given me. I wish also to thank Mr. Harry T. Beddows, Borough Librarian, Shrewsbury, Mr. Kendall of Ellesmere, Mr. C. W. Scott of Weston-under-Lizard, the Rev. J. Talbot of Ellesmere, the Rev. J. L. Vincent of Marbury, the Rev. T. A. Hanson of Rostherne, Mr. E. M. Parker-Jervis of Tabley, Mr. Charles A. Longe of Rostherne, Mr. W. P. Langford-Brooke of Mere Hall, Knutsford, for their information and help.

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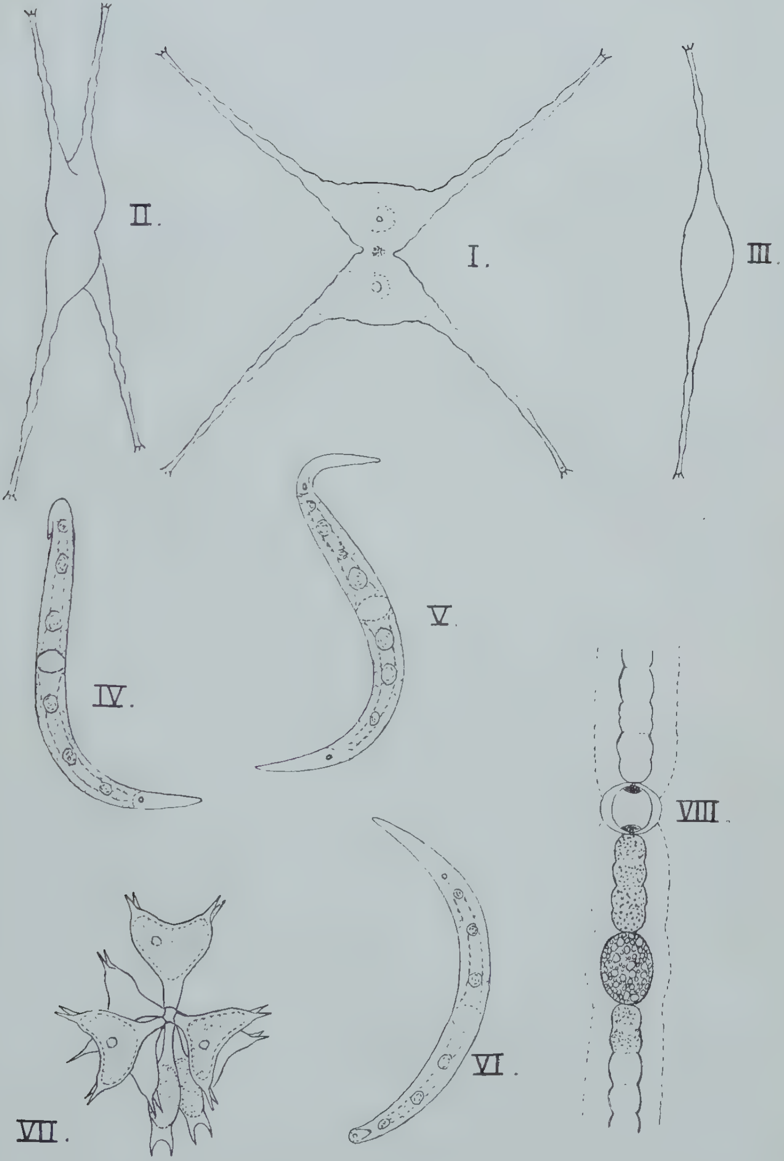
## EXPLANATION OF PLATE 1.

All drawings made with the aid of the camera lucida. Figs. I, II, III, VII × 1160; figs. IV, V, VI, VIII × 650.

Fig. I. *Staurastrum paradoxum* var. nov. *biradiatum*, front view.
II. ,, ,, ,, ,, slightly oblique lateral view.
III. ,, ,, ,, ,, slightly oblique axial view.
IV., V., VI. *Closterium tortum*, sp. nov., showing variations in curvature.
VII. *Sorastrum spinulosum*, form from White Sitch.
VIII. *Anabæna affinis* Lemm., var. nov. *intermedia*.



B. M. G. del.

Grout, photo sc.

SHROPSHIRE, CHESHIRE, & STAFFS. PHYTOPLANKTON.

# Biogeographical Relations of the New Zealand Region.

By W. R. B. Oliver, F.L.S., F.Z.S.

(With 7 Text-figures.)

[Read 2nd April, 1925.]

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## Introduction.

The geographical features which make New Zealand of interest to the plant and animal geographer are the extensive land areas lying in the Pacific Ocean far distant from the nearest continent, the diversity of their physical characters, and the great depth of the surrounding ocean. From a biological view-point the outstanding characteristics of the fauna and flora of the New Zealand region are the absence of mammals, contrasting it with the remainder of the world except Antarctica, the marked dissimilarity of its plant and animal productions to those of Australia, and the presence of an element common to two or more of the southern land masses. No wonder is it, then, that the history of its fauna and flora has often been a matter for discussion among biologists. That New Zealand has been a long time isolated from any other large land mass no one doubts, and that most of its plants and animals are descended from those which reached it over dry land is generally agreed upon by both botanists and zoologists, but in which direction the land bridge or land bridges lay and at what periods they existed are by no means undisputed points.

In the present paper an attempt is made by an analysis of certain classes of plants and animals of New Zealand to determine the countries between which there has been an interchange of species. The main principle underlying the investigation is one consistent with the theory of descent with modification—namely, that each group has had a single place of origin from which its members have dispersed. The place of origin is not necessarily a small locality, but is coterminous with the area occupied by the parent species of the group in question. The present area of greatest development of a genus is assumed to be the place of origin unless other evidence is available to show that it has shifted. The centre of dispersal of a genus is, therefore, not necessarily supposed to remain always at the place of origin. In the case of a genus endemic in the New Zealand region the relations of the family which includes it are made the basis for determining the point of origin of its antecedents, it being assumed that the ancestors of the genus if traced far enough back would be species having closer relations to those of some other country. For instance, the New Zealand endemic genus *Sporodanthus* may be considered as a descendant of a species which would be included in the same genus as the ancestors of *Lepyrodia* with Australia as the centre of dispersal.

Without being in the least concerned with the place of origin and dispersal of the great phyla of plants and animals, it must be conceded that if New Zealand contains or contained faunas or floras which require continuous land for their dispersal then land connection with some other country is proved. But the demanding of land bridges is not to be held to imply that all the present animals and plants of New Zealand or their ancestors have arrived from some other country. On the contrary, the author believes with Dr. Cockayne ('Vegetation of New Zealand,' p. 192, 1921) that many groups have arisen within the New Zealand territory, and further that many species have migrated from it to the surrounding countries.

Before attempting a history of the New Zealand fauna and flora, some general remarks relative to the dispersal of organisms in the Southern Hemisphere will be offered.

## I. Ways of Dispersal.

1. **Land Bridges.**—Most discussions concerning the origin of the fauna and flora of New Zealand, and especially that section of it which has been given the name of Antarctic, have been around the question of former land connections. At one time or another such land bridges have been proposed towards nearly all points of the compass. The easy method by which these hypothetical continents can be brought up from the depths of the ocean has probably been one cause why the study of geographical distribution has made little advance in recent years; for once a land bridge is assumed, there is no incentive to further investigation. Now, land bridges required on

biological considerations should not conflict with geological evidence—that is, the evidence of the structure of the earth's crust. Geologists, I find, generally rely on palæontological evidence when proposing former land connections. Certain geological evidence, however, will be reviewed because it indicates the direction and time of possible land bridges.

*Contour of Ocean-floor.*—On the principle of the permanence of continental and oceanic areas, past land connections would be indicated by submarine ridges.

The broad features of the contour of the ocean-floor in southern regions consist of submarine platforms less than 2000 fathoms below the surface radiating from the Antarctic continent to New Zealand, the eastern Pacific, South America, the central Atlantic, and the south Indian Ocean. A similar extension, but of greater depth, is indicated towards Tasmania, while South Africa is joined to the central Atlantic ridge. The thousand-fathom line completely surrounds the Antarctic continent, so that any direct land bridge with the north must have been at a remote period.

New Zealand is flanked east and west by deep ocean-troughs. Southwards is the broad submarine ridge just mentioned, while northward is a shallower and more broken extension. Sea-bottom under a thousand fathoms is continuous between New Zealand, Lord Howe Island, and New Caledonia. More broken contours connect New Zealand with the western Pacific by way of Norfolk Island and the Kermadecs respectively. Continental connections, according to the evidence of the ocean-floor, are thus indicated from New Zealand to the north and south, but not to the east or west.

Although in the majority of the series of paleographic maps Benson (Trans. N.Z. Inst. vol. liv. 1923) shows a shore-line somewhere near the eastern coast of Australia, he evidently does not consider the Tasman Sea trough a feature of the Palæozoic and Mesozoic periods. But he bases his results largely on the relations of marine faunas, which should be used with caution, as many littoral animals are distributed by means of pelagic larvæ or floating objects and depend more on temperature and ocean currents than coast-lines. Regan has emphasized this point with regard to fishes ('Terra Nova' Report, Zool. vol. i. p. 149, 1916).

The opinion of geologists differ widely regarding the date of origin of the Tasman Sea. Marshall and Morgan think that during the early and mid-Mesozoic era New Zealand was the shore-line of a continent stretching to the westward or north-westward, while Benson draws a map of Australasia in Jurassic times illustrating such a disposition of the land. On the other hand, Arldt, Schuchert, and Stephens (as quoted by Benson) believed the Tasman Sea to have been early formed, existing in the Jurassic period. It should be pointed out that the existence of the Tasman Sea since the Jurassic period is necessary if the former independent junction of Australia and New Zealand with Antarctica during late Mesozoic times be accepted.

*Periods of Elevation in New Zealand.*—Geological evidence points to the late Palæozoic as a period when the New Zealand area was elevated, and the land may have extended so as to join other lands. During Palæozoic times folding, probably pre-Permian, took place along north-west to south-east lines, and at times New Zealand probably formed part of a continent (Morgan, N.Z. Journal Sci. & Tech. vol. v. p. 49, 1922). Recently Park discovered striated boulders in a breccia near Taieri Mouth. He favours a glacial origin, and states that the rocks belong to the Te Anau series, or Upper Carboniferous (Park, Trans. N.Z. Inst. vol. lii. p. 107, 1920).

Glaciation during the Permo-Carboniferous period is known to have been widespread in the Southern Hemisphere. Striated boulders, tillite, or other evidence has been detected in Australia, South Africa, South America, India, and New Zealand In Australia there are two distinct horizons of glacial origin—one, the Kuttung Series, Carboniferous, and the other, the Bolwarra Conglomerate, Permian (David, 'Guide to Hunter River District,' p. 35, 1923). The glacial phenomena would seem to point to the elevation of the land in various portions of the Southern Hemisphere, and thus connections might be made between Antarctica and one or more of the southern continental lands. Such a radial disposition of the land, instead of the east to west direction that the conception of Gondwanaland implies, might explain the distribution of the glacial phenomena in late Palæozoic times.

Stephens believed that during Permo-Carboniferous times eastern Australia and New Zealand were independent groups of islands each united with Antarctica (Proc. Linn. Soc. N.S.W. vol. xiv. p. 349, 1889).

The evidence for an extension of land in Permian or early Triassic times is not clear. It rests on the difference between the fossils of the Maitai (Permo-Carboniferous) and Triassic rocks and on the supposed intrusion of plutonic rocks. In New Caledonia middle Triassic rocks are frequently missing.

A continuous series of sediments, mostly unfossiliferous, covers the period from middle Triassic to lower Cretaceous in New Zealand. The direction of the land from which these are derived has not been ascertained, but whether it be east or west, it might fall within the limits of the submarine plateau on which New Zealand stands—that is, the Tasman Sea might have intervened between the land and the Australian terrain.

The Lower Cretaceous period was marked by intense crustal movement in the New Zealand area, resulting in the folding of all the Mesozoic rocks deposited up to that time. According to Morgan, in the south and in the extreme north of New Zealand the folding followed already existing Palæozoic folding, but elsewhere it commonly took a new direction, north-east to south-west, almost at right angles to the older folding. This was a period of elevation and extension of the land. In New Caledonia no middle Cretaceous rocks are known, so that a long emergence must have been there the feature of that period (Benson, Trans. N.Z. Inst. vol. liv. p. 49, 1923).

Following another period of elevation in Eocene times was a long period of subsidence in the New Zealand area, apparently reaching its lowest limit in the Miocene. Elevation again took place in late Tertiary times, resulting in much block-faulting and tilting.

Summarizing the geological evidence for land connections between New Zealand and other lands, it may be said that elevation is indicated for Permian and perhaps Triassic times, and more certainly in the Lower Cretaceous period. Elevation also took place at the beginning and near the close of the Tertiary epoch. Whether or not land connections with other countries were actually made at any of these periods can best be determined by the biological evidence.

*Marine Faunas.*—I pass over marine faunas as evidence of land connections for the following reasons :—

(1) Marine animals in most cases have free-swimming larvæ, many of them being pelagic. In some groups, larvæ remain in the swimming stage for a considerable time. Mathews records that the young of *Mytilus edulis* hatched on May 21st, 1912, were swimming on August 15th (Journ. Marine Biol. Assn. vol. ix. p. 557, 1913). The pelagic larvæ of littoral molluscs have on several occasions been given distinct generic names, as *Sinusigera*, *Macgillivrayana*, *Chelotropis*, and so on. Many coastal fishes have in their life-history a pelagic phase, which may be the larval state or the young fish. The marine stages of certain freshwater fishes such as *Galaxias* and *Geotria* come under this head.

(2) Even if marine faunas are held to indicate the presence of a coast-line, continuous land connection does not necessarily follow. There may be one or more straits easily crossed by marine animals, especially if the water be shallow but impassable to land plants and animals.

(3) The community of species in marine fossil faunas indicates like conditions of temperature from which the distribution of ocean currents may be inferred. It would scarcely be safe, however, to map land-lines from this evidence, as currents of different temperatures are sometimes found side by side. The marine fauna in the south of New Zealand is different from that in the north. Here are two ocean currents affecting the coast, but they are not separated by a land barrier. A better-known instance of different faunas on the same coast is that of the eastern United States, where the northern and southern faunas meet at Cape Cod. The marine faunas of the present day are limited usually by temperature in a north and south direction and by land barriers in an east and west direction. With a knowledge only of the limits of the Indo-Pacific region from its fauna no one could possibly map the shore-line. An island area like the Pacific would completely baffle any attempt to do so.

*Palæozoic Floras.*—No plant-remains have so far been detected in rocks of Palæozoic age in New Zealand. This, of course, does not mean that land did not exist in or near the area. On the contrary, it is evident that there was land in the vicinity of the South Island where fossiliferous rocks of Ordovician, Silurian, and Permian ages occur.

Prior to the late Carboniferous the vegetation of the world was nearly uniform in character. For such a flora, land connections are not indicated in any particular direction. Junctions along lines indicated by present-day ridges would be as good an hypothesis as any other. Similarly, an outward movement from Antarctica along radial land connections before the advancing cold would explain the distribution of the *Glossopteris* flora.

*Mesozoic Floras.*—In several localities in New Zealand floras of Mesozoic age have been described. But up to Jurassic times one type of flora was world-wide in distribution. Land connections in any definite direction, therefore, are not to be inferred from such a flora. That New Zealand was before Triassic time connected with other countries and shared their vegetation is evident enough from the presence of a varied flora of Gymnosperms besides numbers of fern-like plants and Equisetales.

*Present Fauna and Flora as indicating land connections.*—The existing fauna and flora of New Zealand constitute a complex made up of (1) the descendants of species of plants and animals which occupied the New Zealand territory when it was connected with other lands, and (2) species that have arrived overseas or are descended from species that have arrived overseas. It may safely be said that both these groups contain endemic genera and species—that is, true New Zealand plants and animals that attained their independent rank in the area in which they are now found.

That a connection by continuous land between New Zealand and some other country is necessary to explain the presence of a large proportion of the flora and fauna, is admitted by all. But in what direction the connection or connections lay, at what period in the earth's history they took place, and which plants and animals entered or left New Zealand by such connections are and may always remain matters of contention and conjecture. It is evident, however, that the key to the origin of the present fauna and flora of New Zealand lies in the past changes in the distribution of the land and in the climate, and that the evidence for these must in the first place be biological (including palæontological), but must not conflict with geological evidence. Huxley long ago said that it would be for the morphologist to give the casting vote on questions of geographical distribution.

**2. Ocean Currents.**—Granting no connection of the Antarctic continent with land to the north during the Tertiary epoch, except perhaps Graham Land and South America, there would be little alteration in the main currents in the southern ocean to what obtains at present. As the circulation of the atmosphere is in its main features governed by the position of the sun and the rotation of the earth, it may be presumed that the direction of the prevailing winds have not greatly changed. Assuming, then, that the land at its greatest extent was not more than shown in the map herewith (p. 136), there would be throughout the Tertiary period westerly winds or easterly-moving storms in the south temperate region. The surface currents in accordance with the atmospheric circulation would carry drift in an easterly direction, and an interchange might easily take place between the Antarctic continent and the New Zealand and Australian continents.

The direction of the drift of the surface water of the Southern Ocean at the present day is evidenced by the general northward and eastward movement of icebergs from Antarctic regions. In the South Pacific they reach the latitude of New Zealand. Icebergs have been stranded at the Chatham Islands. In the South Atlantic and Indian Oceans, icebergs pass the 40th parallel of South latitude. Antarctic animals are sometimes stranded on the shores of New Zealand and Australia. The crab-eating seal, for instance, has been recorded twice in New Zealand and twice in Australia. Possibly, however, the northward drift from the Antarctic continent in early Tertiary times when the coast at least supported vegetation may not have been so pronounced as it is now.

The investigations of Guppy ('Plants, Seeds, and Currents in the West Indies and Azores,' p. 310, 1917) show that, from the present direction of currents in the Southern Hemisphere, Australia would receive drift from Fuegia, the islands of the Southern Ocean, and South Africa, and distribute it to the north of New Zealand: while New Zealand would receive drift from Fuegia, the Antarctic continent, the islands of the Southern Ocean, Tasmania, and Southern Australia, and its southern end would distribute it to South Chile.

At present a warm current runs south along the east Australian coast, turning about the latitude of Tasmania towards New Zealand. This current would not come into existence while the Tasman Sea was closed to the north. Instead, the easterly current might be deflected northwards on reaching the New Zealand continent, and coast round the Tasman Sea, carrying drift to Australia.

*Drifting Pumice.*—There is an agent of dispersal sufficient to account for the transference of coastal marine forms to all parts of the Pacific, namely drifting pumice. It is cast up on the shores of Australia, New Zealand, and all the islands of Polynesia, and supports corals (Kent, 'Great Barrier Reef,' p. 122, 1893), barnacles, and no doubt many other forms of marine life.

3. **Atmospheric Conditions.**—The dominant feature of the climate of the south temperate regions is the passage past any given point of a series of easterly-moving cyclonic storms. They take a more southern route in winter than in summer. A second type of cyclonic storms comes to New Zealand from the north-west and affects the northern portion of the Dominion. These are usually summer visitors. The rate of movement of cyclonic storms varies considerably, but averages about 400 miles per day (Pemberton, N.Z. Journ. Sci. & Tech. vol. ii. p. 165, 1919).

The path of cyclonic storms in the late Tertiary period would depend on the extent of the glaciated area of Antarctica, for these storms coast round the anticyclone area of the polar ice-cap. During the Pleistocene glaciation, therefore, they would be considerably farther north than at present.

4. **Animals.**—Birds as an agent of dispersal need only be referred to here by noting that the Southern Ocean swarms with long-distance flying petrels, which breed in countless numbers among scrub and tussock vegetation on the Subantarctic islands. Probably occasional opportunities are given for the transference of seeds of plants and eggs of animals from island to island by these birds.

## II. Means of Dispersal.

All land plants pass through a stage in their life-history specially fitted to endure unfavourable conditions. In spermophytes it is the seed, in pteridophytes and lower plants the spore. It is during this stage that dispersal most effectively takes place, and the opportunity is given for transportation over long distances. A classification of plants according to whether seed or spore carriage is by wind, water, or animals would be based on inference rather than on observation or experiment; moreover, the seeds or spores of a species might be carried by more than one of these agents. In the following analysis I have given in percentages certain particulars of the floras of Australia and New Zealand and of the non-endemic vascular plants in New Zealand. Figures are first given for those systematic groups which appear specially fitted for wide dispersal—namely, the pteridophytes, orchids, composites, grasses, and sedges. The remainder of the New Zealand plants are then divided according to whether the fruit is fleshy or dry. The results are apparently contradictory, but when other factors, such as the general direction of the movement of plants in the Southern Hemisphere and the age of the groups, are taken into consideration, explanations may be given for these apparent anomalies.

| | Australia.<br>10,670 species. | New Zealand.<br>1570 species. | New Zealand non-endemic.<br>370 species. |
|---|---|---|---|
| Pteridophytes ...... | 3 | 10 | 26 |
| Orchids .......... | 4 | 3 | 4 |
| Composites ........ | 6 | 14 | 5 |
| Grasses .......... | 4 | 7 | 8 |
| Sedges .......... | 4 | 8 | 12 |
| Plants with fleshy fruits. | 79 | 14 | 3 |
| Plants with dry fruits not elsewhere included. | | 44 | 41 |

The first three groups are specially adapted for dispersal by wind, yet each gives a different result when the New Zealand non-endemic species are compared with the floras of Australia and New Zealand. The high proportion of pteridophytes is what might be expected in plants with minute spores capable of being carried long distances by wind. Orchids show no similar high proportion, perhaps because they are a group recently evolved and much specialized. Composites in the New Zealand non-endemic plants show a proportion similar to that of orchids when both are compared with the Australian flora, but when compared with the New Zealand flora they are found to be only about one-third as numerous. They are probably an old group, but they show a greater development in New Zealand than in Australia, and, as will be pointed out later, migration in the south temperate region is mainly from west to east. Hence the proportion of composites found in the New Zealand non-endemic plants, which are mainly also Australian, is low.

The seeds of grasses and sedges may be carried by all agencies, but mainly perhaps by wind and animals. Both, as might be expected, are well represented in the New Zealand non-endemic species. Plants possessing fleshy fruits are usually considered as specially adapted for dispersal by animals. It is significant, therefore, that the proportion of these in the New Zealand flora, which I consider a continental type, is high, while the percentage in the New Zealand non-endemic plants is quite low.

As most plants are capable occasionally or accidentally of crossing stretches of water, I do not rely greatly on means of dispersal to judge whether they require continuous land connections to explain their present distribution. Rather do I contend that where there has been connection by land the flora which occupied it will, when afterwards divided, show by comparison of the separated parts that they were originally one. The common element will be large and fundamental. There will not be two distinct floras each having but fragments of the other, as appears when the floras of Australia and New Zealand or New Zealand and South America are compared. In one case original continuity of the land is indicated, in the other it is not.

## III. THE MOVEMENT OF SPECIES.

*Life of a Species.*—A point to be considered in connection with the movement of species is the length of life of a species. A species changes in the course of time; so that whether it gives rise to more than one or not, it eventually changes into what would be considered a distinct species, provided of course it does not become extinct. This statement requires modifying only by saying that some species change more quickly than others. In a change such as this it is evident that isolation is an important condition in originating new species, for those individuals which are free to cross will determine the limits of the changing species. The palæontological records show that very few species exist as long as the duration of the Tertiary era. From this it follows that if a species is found in lands presumed to have been separated during the whole of the Tertiary period, the probability is that dispersal of that species between the countries in which it is now found is still going on.

The phenomena of swamped genera—that is, those non-endemic but represented in New Zealand by endemic species only—naturally follows from the fact of species changing in course of time, in this case the New Zealand section of the original species running its own course through isolation. Many genera and more species have come into existence as such in the New Zealand region, and the process is still going on.

The age of very few recent species of New Zealand plants can be known, as the palæontological records are scanty. In some cases the relative ages of two groups may be judged by morphological characters, but always with a degree of uncertainty. Willis's 'Age and Area' hypothesis may be useful in suggesting the relative ages of species or the length of time they have been in New Zealand, but independent confirmation is needed.

It should be borne in mind that the disentanglement of the present flora and fauna is complicated by the fact that dispersal has been continuous throughout the ages. Species have arrived and species have departed. There appear, indeed, to be regular migration routes.

*Similar varieties arising in two or more localities.*—Although it is conceivable that a species under similar conditions in two widely-separated countries might in each give rise to varieties which on comparison would appear identical, it is improbable that the new varieties would continue to remain alike for long. The tendency would always be towards differentiation into distinct species. Thus Guppy believes that the variety *Cataractæ* of *Carex Œderi* found in New Zealand, South Africa, and South America is a corresponding varietal modification which has taken place in each region. Likewise I have recorded my opinion that the similarity of the mountain species of *Coriaria* (*C. thymifolia* in the Andes and *C. lurida* in New Zealand) may be due to the fact that each is a derivative of the widespread *C. ruscifolia* (Trans. N.Z. Inst. vol. liii. p. 365, 1921).

*Single point of origin.*—If the plants and animals of New Zealand be examined from the point of view of their probable place of origin and subsequent dispersal, a basis will be established for determining the origin and movements of the flora and fauna. For, assuming the members of a family or generic group to be derived from a common ancestral species, a single point of origin and dispersal follows. The region where the greatest development of a group occurs will usually be where the group originated, but the centre of dispersal may shift. In this case indications of the place of origin may be traced by considering the relationships of the group in question, as in the families Stylidiaceæ and Restiaceæ to be mentioned presently.

In very old groups there are probably several whose greatest development is now in the Southern Hemisphere, though they originated in the Northern Hemisphere, where some of them are found fossil in Cretaceous and Tertiary rocks. Some of the Coniferales, as *Agathis*, *Araucaria*, and *Phyllocladus*, also *Fagus* (including *Nothofagus*), appear to come under this category. The principle of the spreading out of successive waves of migration, each a stage higher than the preceding one, so that old types are found farthest from the centre of dispersal, has been recently pointed out by Matthew (Ann. N.Y. Acad. Sci. vol. xxiv. 1915).

Willis ('Age and Area,' p. 60, 1922) has discovered an important fact in plant-distribution—namely, that if the endemic species of a country be arranged according to the size of their areas of distribution, then more occupy small than large areas. This gives strong support to the principle of a single point of origin for each species. Willis concludes that the older a species the wider its distribution. There can be little doubt, however, that agents for dispersal and opportunity for establishment are the deciding factors in determining the area a species occupies.

In a family, as it extends its area, new points of dispersal arise. Thus the family Stylidiaceæ (or Candolleaceæ) presumably originated in Australia, where nine-tenths of the species are now found, and spread thence eastward. Reaching New Zealand, a new point of dispersal was formed, resulting in the multiplication of the species of *Forstera*, and the origin of *Oreostylidium* and *Phyllachne*. Even if it be argued that these two genera may have arisen in Australia, travelled to New Zealand, and subsequently became extinct in Australia, it makes only a difference of degree—namely, whether the ancestral species when they crossed the Tasman Sea area were differentiated as genera or not. *Phyllachne* has reached still farther eastward as far as South America. Equally interesting results are obtained from a study of the family Restiaceæ, which probably originated in South Africa, where most of the genera and species are now found. Some genera like *Restio* and *Hypolæna* have species in both countries but fewer in Australia; *Leptocarpus* has more species in Australia than in South Africa, and there are eleven genera of small and medium size confined to Australia. The further extension of the family eastward to New Zealand is precisely of the character of its extension from South Africa to Australia. Of the three species in New Zealand one belongs to an endemic genus, *Sporodanthus*, related to a genus, *Lepyrodia*, endemic in Australia; another, *Leptocarpus simplex*, is endemic, but belongs to a genus mainly Australian; while the third, *Hypolæna lateriflora*, is identical with an Australian species, and the genus is mainly South African. The distribution of the whole family harmonises with the theory of origin in South Africa, dispersal to Australia by chance crossings during a long period of time, and thence extension to New Zealand in a similar way with long intervals between the arrival of the species.

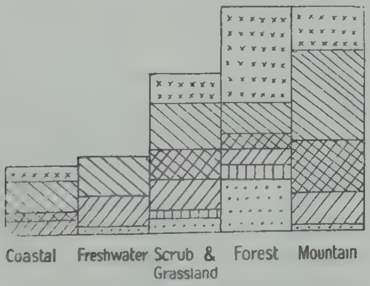
## IV. The Movement of Floras and Faunas.

*Descent of Faunas and Floras.*—A fauna or flora, like an individual, is the lineal descendant of a previous fauna or flora that in course of time has been modified by inherent changes in the species, and by immigrations and emigrations due to changes in climate or other causes. The study of past floras and faunas, especially of the Tertiary period, amply justifies this principle. The Eocene gymnosperms of New Zealand are more closely related to existing species than are those from the Cretaceous. The theory of Ettingshausen that the Tertiary floras of Australia and New Zealand resembled that of Europe more than they resembled the present floras of Australia and New Zealand, has gained wide acceptance notwithstanding the fact that it has either been rejected or ignored by most botanists who have since discussed the relationships of the floras. Ettingshausen's theory rests on the identification of fossil leaves, which shows how the use of characters of small taxonomic value may lead to results inconsistent with the principles of distribution and descent. In point of fact, if Ettingshausen's identifications be accepted, his conclusions would scarcely be justified, as the Tertiary floras of both Australia and New Zealand contain large elements related to the existing floras and not to that of Europe. The reference of European Tertiary species to southern genera like *Eucalyptus* has been discredited and needs revision, as does also the reference of Australian and New Zealand Tertiary plants to northern genera.

*Migration of Floras.*—In order to make comparisons of different floras with a view to determining those which migrated as a whole and those which have been transferred by occasional means, I have made a comparative analysis of the vascular floras of New Zealand, Lord Howe Island, the Kermadec Islands, and the plants common to New Zealand and Australia and New Zealand and South America (see p. 140). First the plants were divided into five main groups according to habitat—namely, (1) coastal, including all coastal formations subject to the influence of salt air or water; (2) freshwater, comprising swamp, lake, and bog associations; (3) scrub and grassland below the upper limit of forest; (4) forest; and (5) mountain formations, including scrub and grassland above the upper limit of forest. The South Island of New Zealand was taken as the basis for the definition of mountain plants. It was necessary to have some criterion such as this because such mountain plants as reach the islands of the Southern Ocean there descend to sea-level. Each of these five main groups was next divided according to their method and opportunities for dispersal thus: Plants belonging to four groups based on systematic affinity were first counted; these groups are pteridophytes, orchids, grasses, sedges and rushes, and composites. The balance were counted according to whether they were herbs or woody plants. This grouping is admittedly mixed, being based partly on systematic and partly on ecological characters. But from the point of view of dispersal they are comparable, and the features brought out by this classification are, I believe, of some value. Each flora was therefore divided into thirty parts; these were then reduced to percentages and plotted in the accompanying diagrams. The total area is the same in each diagram. For explanation of the diagrams see fig. 6, p. 134.

*The New Zealand Flora* (fig. 1).—New Zealand is an extremely diversified country with a long and varied coast-line, abundance of freshwater streams and lakes; scrub, grassland, and forest extensively developed in both islands; and large areas of mountain country in the South Island, with a smaller area in the North Island. Its flora, therefore, might well serve as a standard for comparison with those of other countries, but my investigations have not led me so far. The percentages of the five main groups utilised in the classification adopted comes very near to multiples of tens, there being two groups each about 10 per cent. of the flora, coastal and freshwater plants; one about 20 per cent., lowland scrub and grassland; and two, each 30 per cent., forest and mountain. The composition of these groups may now be considered. The leading features are these:—There is a small proportion of woody plants in the coastal group, the bulk being herbs, grasses, and sedges. The freshwater plants are about half herbs and about half grasses and sedges. In lowland scrub and grassland all groups are fairly well represented. The composition of the forest is important from a distributional standpoint, as the characteristics of forests in continental masses and in oceanic islands differ essentially in features which I have endeavoured to portray. I infer, therefore, that the forest on an island having the same characters as that of a land mass would indicate that it migrated thither by a continuous land connection. The New Zealand forest contains 43 per cent. of woody plants, 23 per cent. of pteridophytes, and the balance about equally divided between the other groups of orchids, grasses, composites, and herbs. The New Zealand mountain plants are strong in woody plants, herbs, and composites.

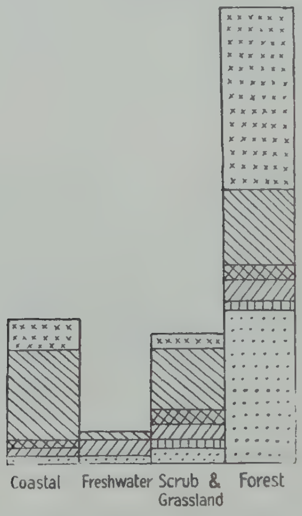
FIG. 1.



New Zealand Flora (see p. 134).

*Lord Howe Island Flora* (fig. 2).—The flora of Lord Howe Island is introduced for comparison with that of New Zealand because the island has at one time been in direct land connection with New Zealand and New Caledonia, but has been a long time, perhaps for the greater portion of the Tertiary period, isolated and hence subject to oceanic conditions as regards dispersal. The flora then should exhibit the characters of a large land area with oceanic elements added, and such, I believe, the analysis here diagrammatically given shows. The island is almost entirely covered with forest, which reaches to the highest point; hence mountain plants are absent. Freshwater conditions are likewise scarcely represented. The percentage of plants in the coastal group is twice as high as in New Zealand This would follow from the greater length of coast-line in proportion to area in the two places. The scrub and grassland group is smaller than in New Zealand, but, like it, contains representatives of all the classes of plants, herbs being especially abundant. The scrub on Lord Howe Island is mainly found on the high cliffs. Forest is naturally the chief feature of the vegetative covering of Lord Howe Island. Comparing it with that of New Zealand, it is found to contain 40 per cent. of woody plants and 33 per cent. of pteridophytes, with representatives of all the other groups. In its proportion of woody plants it comes close to the forest of New Zealand, but the percentage of pteridophytes is much higher. Here is evident the influence of oceanic conditions, as the additions to the forest flora since Lord Howe Island formed part of the land bridge to the north of New Zealand would naturally be plants such as ferns, which were able to be transported over oceanic areas. It is also significant in this connection that the proportion of herbs in the Lord Howe Island forest is higher than it is in the New Zealand forest. The forest of Lord Howe Island, then, bears the stamp of having migrated there overland and of having been added to afterwards by occasional means of transport.

FIG. 2.



Lord Howe Island Flora.

Further evidence of the former connection of Lord Howe Island with New Zealand and New Caledonia is furnished by the presence of a flightless rail, *Tricholimnas sylvestris,* and several species of large land shells, including *Placostylus bivaricosus* (see Oliver, Trans. Inst. N.Z. Inst. vol. xlix. p. 111, 1917).

*Two Floras in New Zealand.*—The analysis so far given does not disclose the presence of different floras in the same area. In New Zealand, for instance, there appear to be intermingled two floras, one in which podocarps, pines, and trees of Malayan affinities are dominant, and another in which *Nothofagus* is the prevalent tree. But the plants associated with *Nothofagus* are likewise mainly plants of Malayan alliances, so that the distinctness of the two types of forest is probably due to age. One is the result of an earlier period of prevalence in New Zealand than the other, the *Nothofagus* forest being the earlier. It has for the most part been displaced by the mixed forest. Both forests are similar in the characters brought out in the diagram, so that both are of continental type. Were the *Nothofagus* forest to be the portion of a forest invading New Zealand from the south, it should be accompanied by a flora of southern facies, South American for instance, and one would expect it to be best represented in the islands to the south of New Zealand. Such, however, is not the case. The forest of the Auckland Islands does not even include *Nothofagus* as one of its members. Its dominant tree is the southern rata, *Metrosideros lucida,* a tree belonging to a genus of Malayan origin.

*Disharmonic Floras.*—If a flora of the constitution of that of New Zealand be termed harmonic, then one departing from it in the character and proportion of all its main groups, but especially of its forest, may be called disharmonic. This term I have borrowed from the writings of zoogeographers, for the floras which cross stretches of ocean by occasional means of transport obey different laws to those which migrate overland. They are the result of an accumulation of species which have accidentally come together; hence they would be expected to lack some of the essential characters of harmonic floras and have others enhanced. Such a disharmonic flora is that of an oceanic island—that is, one that has received its entire flora overseas. Coastal and freshwater floras exhibit no such differences as those found between continental and oceanic forests, but scrub and grassland differ to a small extent in continental and island areas. Before analysing a typical island of the oceanic class, some general remarks on the migration of plants in the southern temperate region will be made.

*Plant-formations and wide dispersal.*—Widely-distributed species of plants are in nearly all cases those belonging to plant-formations which are more or less open and exposed. Forest plants usually are not widely distributed. The reasons for this probably are that the opportunities for having their seeds removed by wind or birds, or, in the case of coastal formations, by ocean currents, are best afforded in low, exposed formations. The opportunities for establishment are likewise more frequent in open formations than in closed ones. Hence coastal, swamp, scrub, and mountain plants make up the bulk of the widely-ranging species common to two or more of the southern land masses.

The wide distribution of freshwater plants has often been commented on. They form 10 per cent. of the flora of New Zealand, 25 per cent. of the 320 species common to Australia and New Zealand, and 35 per cent. of the 80 cosmopolitan species in New Zealand. Thus the wider ranging the group the higher the percentage of freshwater plants.

Certain portions of White Island off the north-east coast of New Zealand are each summer occupied by gannets, which destroy the vegetation where they breed. When they leave the island a rank growth of herbs springs up in their place. The seeds of these have without doubt been carried, probably by wind and birds, from the mainland, but the birds have made the opportunity for their establishment.

*Distribution in Temperature Zones.*—On comparing the distribution in their respective countries of plants and animals common to Australia and New Zealand, some are found to be restricted to belts bounded by isothermal lines. For instance, a few marine molluscs of southern distribution in Australia are found in the same latitudes in New Zealand. *Mytilus planulatus* and *Argobuccinum tumidum* are examples. Similarly *Tonna cerevisina*, *Ostrea cucullata*, and *Mitra carbonaria* occur in the north of New Zealand and in corresponding latitudes in Australia. Plants found in Tasmania but not in Australia and with a southern distribution in New Zealand are *Gaultheria depressa*, *Donatia Novæ-Zealandiæ*, *Utricularia monanthos*, *Liparophyllum Gunnii*, and *Hierochloe Fraseri*. Among those found in Australia but not in Tasmania and with a northern distribution in New Zealand are *Calystegia marginata*, *Bromus arenarius*, *Sparganium subglobosum*, *Cassytha paniculata*, and some orchids. These species are mentioned to show that distribution has probably taken place direct across the Tasman Sea, as those plants of southern distribution could not tolerate migration by way of a land bridge in a warmer region. Most species are more generally distributed on both sides of the Tasman Sea than those just mentioned, and this would naturally be the case with plants and animals that have the means of crossing an expanse of ocean.

*The West to East Movement.*—Perhaps the most important movement of organisms migrating by means of wind, currents, or animals in the south temperate region is that in an easterly direction. It is specially evident in plants where large genera in the continental regions have one or two outliers to the eastward. For instance, many Australian genera containing up to 60 species (*Persoonia*) have a few representatives in New Zealand. *Phebalium*, *Leptospernum*, *Haloragis*, *Epacris*, and others may be mentioned. Large

New Zealand genera like *Hebe** and *Coprosma* have one or two species in South America. There are South African genera like *Hypoxis*, *Tetragonia*, *Mesembryanthemum*, *Restio*, *Hypolæna*, and *Wahlenbergia*, with few species in Australia; while there is a regular trail of Fuegian plants eastwards to the Falklands, South Georgia, and other subantarctic islands.

*The East to West Movement.*—This is very small when compared with that from west to east. Possibly it may be accounted for by occasional bird carriage or upper air currents. Outlying species of the New Zealand genera *Celmisia*, *Ourisia*, *Hebe*, and *Psychophyton* are found in Tasmania. The Australian genera *Hibbertia*, *Keraudrenia*, and *Rulingia* each have one or two species in Madagascar.

*The Flora and Fauna of Oceanic Islands.*—The study of the plants and animals of islands which on geological evidence appear never to have been united with a larger land area should throw light on the nature of those which are able to cross wide expanses of ocean. The Kermadec Islands may be taken as an instance. According to my own observations (Trans. N.Z. Inst. vol. xliii. p. 524, 1911), these islands have been built up of volcanic materials on a submarine bank. Their plants and animals must therefore all have crossed at least 600 miles of ocean. And it is significant that the bulk of them are related to species found in New Zealand, from which direction come the prevailing winds. The surface currents, as evidenced by logs of New Zealand origin cast up on Sunday Island, flow in the same direction. The vascular plants of the Kermadecs consist of 38 pteridophytes, 20 grasses and sedges (including *Juncus* and *Typha*), 2 orchids, 9 composites, 27 other herbs of which 17 are coastal and none forest, and 18 woody plants of which 14 are forest. Included in the foregoing total are 9 species with succulent fruits. The flora is fragmentary in the sense that there are only one or very few to each genus, and large New Zealand genera, such as *Hebe* and *Coprosma*, are represented in this way. Thus, although most ecological groups occur in the Kermadecs, including trees with succulent fruits which almost certainly depend for their transference on birds, most of the species are ferns, grasses, sedges, composites, and plants of open formations. Of the 114 species, 86 are found in two or more of the adjacent regions of Australia, Polynesia, and New Zealand (see Oliver, Trans. N.Z. Inst. vol. xlii. p. 149, 1910).

The main features of the flora are shown in the diagram (fig. 3). The proportion of coastal plants is much higher than in Lord Howe Island. This, of course, is due to the fact that ocean currents are one of the means of transport, and the land plants depending on occasional means of dispersal number less than half as many as in Lord Howe Island. The coastal plants of the Kermadecs include relatively more composites, grasses, and sedges than do those of Lord Howe Island. Freshwater plants are few and mountain plants altogether wanting. The scrub plants of the Kermadecs compare with those of Lord Howe Island, though exhibiting a higher proportion of pteridophytes and composites. Even here the insular character of the flora is evident. But it is in forest plants that the Kermadecs differ essentially from continental forests such as Lord Howe Island and New Zealand. The proportion to the whole flora is high because practically the whole island is under forest. The proportion of species of trees in the forest, which is 43 per cent. in New Zealand and 40 per cent. in Lord Howe Island, falls to 30 per cent. in the Kermadecs, whereas the percentage of pteridophytes in the forest, from 23 in New Zealand and 33 in Lord Howe Island, rises to 60 per cent. in the Kermadecs.

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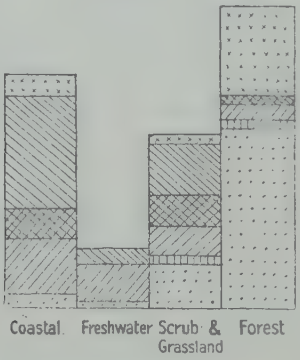
* The following groups are here used in a generic sense, though appearing only as sections of genera in Cheeseman's 'Manual of the New Zealand Flora,' 1906:—*Hebe*, *Pygmæa* [both = *Veronica*], *Schizeleima* [= *Azorella*], *Edwardsia* [= *Sophora*], *Gymnelæa* [= *Olea*], *Leucogenes* Beauv.

Fig. 3.

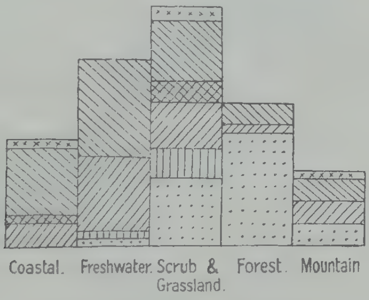


Kermadec Islands Flora.

*Plants common to Australia and New Zealand* (fig. 4).—In the light of results obtained by comparing the floras of oceanic islands like the Kermadecs with continental floras on a large land mass as in New Zealand or isolated as on Lord Howe Island, it will be profitable to analyse in a similar way the plants common to New Zealand and other countries. Beginning first with those found in Australia or Tasmania and New Zealand, 320 in number, they may be expressed in diagrammatic form as with the floras already discussed. Coastal plants are in the percentage to the flora here under examination midway between those of New Zealand and Lord Howe Island, with a composition similar to the latter. Freshwater plants occur in large proportion, 25 per cent. of the flora, and consist of nearly half herbs and two-fifths grasses, sedges, and rushes. As has already been pointed out, freshwater plants are apparently easily transported over oceanic areas, so that their fewness on Lord Howe Island and the Kermadecs must be due solely to the fact that the conditions required for their establishment are there of small extent. Scrub and grassland plants are well represented, and in their composition resemble very closely those of the Kermadecs. Forest plants consist of 75 per cent. pteridophytes and the balance herbs, grasses, and sedges. The mountain plants form the smallest group, but this may be explained by the fact that these plants are but a small proportion of the vegetation of south-eastern Australia and Tasmania.

Comparing the plants common to Australia and New Zealand with those of the Kermadecs, it will be seen that in those characteristics by which the flora of the Kermadecs differs from that of New Zealand, the Australian element in the New Zealand flora differs in a still greater degree. It is indeed more "oceanic" in character than the flora of an oceanic island. This element is of course complex, consisting of species which have reached New Zealand and Australia independently from the Malayan region, species which have reached New Zealand overseas from Australia, and species which have migrated in the reverse direction.

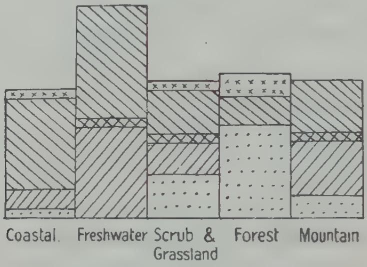
Fig. 4.



Australia–New Zealand Fauna.

*Plants common to New Zealand and South America* (fig. 5).—Now compare the diagrammatic representation of the 70 species of plants common to New Zealand and South America with that of the 320 common to Australia and New Zealand. In the relative proportions of the five main ecological groups there is an apparent difference owing to the different proportions of the scrub and grassland and mountain groups. But this is due to the latitude in which dispersal takes place, for the scrub and grassland plants of the islands of the southern oceans are mountain plants in New Zealand and are counted as such for the purpose of the diagrams. Now, these form a large proportion of the plants common to New Zealand and South America. Hence, if the scrub and mountain groups be counted as one, the agreement of the diagrams is remarkably close. The percentages for the Australian element in the New Zealand flora are coastal 14, freshwater 25, scrub and grassland 42, forest 19. In the South American element the corresponding figures are 17, 28, 36, and 19. The components of these groups are also in the two elements quite similar. The most noticeable difference is in the forest group, there being in the South American element two trees. These are *Edwardsia microphylla* and *Coriaria ruscifolia*, both species which at the present day are, there can be little doubt, actually being dispersed, both being found on intermediate islands in the Pacific Ocean. Guppy found that the seeds of *Edwardsia microphylla* germinated after floating for seven months in sea water. *Coriaria ruscifolia* is a plant of open scrubland more than of forest, and bears numerous small succulent fruits which are greedily eaten by birds, though the chances of these being carried by sea-birds would possibly be through sticking to the plumage.

Fig. 5.



New Zealand–South America Flora.

Taken as a whole the plants common to New Zealand and South America belong to groups comparable in their characteristics with those common to New Zealand and Australia, and they exhibit in a high degree those features which characterise the floras of oceanic islands. In reality, as will appear in the final part of this paper, the South American element in the New Zealand flora is a complex one, consisting of (1) species which have reached both countries by migration from the Northern Hemisphere, (2) species which have migrated from New Zealand to South America overseas, and (3) species which have migrated from South America to New Zealand overseas. The possibility of any of the species of plants at present common to New Zealand and South America being due to their having crossed by a direct land connection is not here admitted.

## V. HISTORY OF THE NEW ZEALAND FLORA AND FAUNA.

1. **Mesozoic Floras.**—It is insisted by all who study them that the Triassic and Jurassic floras are similar in type throughout the world. They are known from all the continental masses, including Antarctica and New Zealand. As in the earlier floras, therefore, land connections in any definite direction are scarcely indicated. Of the Jurassic plants known in New Zealand six extend to the British Isles, six to India, nine to Australia, and five to Graham Land. The species common to Australia and New Zealand are

given by Arber (N.Z. Geol. Surv. Pal. Bull. No. 6, p. 24, 1917) as follows: *Cladophlebis australis*, *Thinnfeldia lancifolia*, *T. odontopteroides*, *T. Feistmanteli*, *Tæniopteris Daintreei*, *T. crassinervis*, *Coniopteris hymenophylloides*, *Sphenopteris Currani*, *Ectocladus conferta*. Of these, *Ectocladus* belongs to the Coniferales; the remainder are fern-like plants and may be seed-bearing; further, of the 45 Mesozoic plants known from New Zealand, six are Cycadofilices, eight Coniferales, and of the 27 fern-like plants included in the remainder many may prove to be seed-bearing. A land connection is therefore demanded with some other portion of the world. Nine species of the New Zealand Mesozoic plants occur in the Upper Triassic (Rhætic) beds, which would place the land bridge before this time. It might well have occurred during the early Triassic period when on geological evidence, according to Marshall, Park, and others, a break in the faunal succession and a period of orogeny took place. As to the direction in which this land bridge lay, it is not necessary to assume that there was continuous land in temperate regions joining New Zealand and Australia. This is suggested by Arber and mapped by Benson, though Arber states that the comparison of the New Zealand with the Australian and Tasmanian Jurassic floras is more remote than might be anticipated. An extension of land to the north along the route afterwards taken by the Malayan flora would be the probable connection in early Mesozoic times.

2. **Malayan Land Connection.**—A large proportion of the plants and animals at present living in New Zealand, perhaps the bulk of them, are such as require continuous land connection for their dispersal. Their presence demands that at some period in the past, New Zealand was joined to the other land mass of the globe. Most of these animals and plants are related to species now found in lands to the north, and an explanation of the origin of these must be consistent with the fact of the fundamental differences between the faunas and floras of the south temperate land masses.

*Distribution of Coniferales.*—The distribution of the Australian and New Zealand Coniferales must be considered here. The presence of all may be explained on the assumption of a northern origin. *Araucaria*, *Agathis* (=*Dammara*), *Libocedrus*, *Podocarpus*, and *Phyllocladus* or allied forms all occur in the Cretaceous and Tertiary of Europe and North America. Thus their presence in the southern land masses is explained by migration along land lines from the north. Knoche (Etude Phytogéogr. Iles Baléares, p. 155, 1923) holds this view regarding *Libocedrus* and other genera. The only other New Zealand genus, *Dacrydium*, is represented by several species in the Malayan region and New Caledonia. There are seven species in New Zealand, one in Tasmania, and one in Chile. Fossil species have been described from New South Wales and New Zealand.

The Australian genera include all those in New Zealand except *Libocedrus*, and, besides these, six genera confined to Australia and Tasmania. *Diselma*, *Microcachys*, and *Athrotaxis* are found in Tasmania only, the first two, and *Pherosphaera* with one species in Tasmania and one in New South Wales, are closely related to *Dacrydium*. *Athrotaxis* had allies in the Tertiary of Europe. *Callitris* and its ally *Actinostrobus* are related to African genera. The Coniferales, being an old order, show a good deal of diversity both in Australia and New Zealand. The congregation of genera in Tasmania perhaps shows, as in the case of New Zealand, some former land extension followed by contraction. The joining up to Australia and subsequent separation would possibly account for this.

*Distribution of* FAGUS.—The history of *Fagus* (including *Nothofagus*) is apparently precisely similar to that of *Araucaria* and *Agathis*. *Nothofagus* differs from *Fagus* only in the smaller size of the flowers and leaves and in the fewer flowers in the male catkins. Some species in Australia (*F. Moorei*) and South America have large leaves. It is found in South America (8), Tasmania and Eastern Australia (3), and New Zealand (4 species and several hybrids), whereas *Fagus* is confined to the north temperate region, including Japan. But *Fagus* has been described from the Upper Cretaceous of Kansas and various Tertiary localities in the United States, British Columbia, Alaska, and Europe. Fossil plants assigned to both *Fagus* and *Nothofagus* have been described from the Oligocene of Graham Land, whilst possibly certain Tertiary plants from Australia and New Zealand may, as Ettingshausen believed, be referred to *Fagus*. It is probable that *Fagus* and *Nothofagus* originated in North America and spread thence east, south, and west. The western moiety passed, *via* Japan, round the Pacific, reaching Australia and New Zealand. A similar place of origin and routes of dispersal would explain the past and present distribution of *Araucaria* and *Agathis*. But these two genera have become extinct in North America, whereas *Fagus* still persists. If the characters by which *Nothofagus* is separated from *Fagus* be considered primitive, then these two genera exemplify the principle enunciated by Mathew, which states that a group should be most advanced at its point of original dispersal, the most conservative stages being farthest from it. I find that Guppy believes in the northern origin of the New Zealand and South American species of *Fagus* (including *Nothofagus*) (Plants, Seeds, and Currents in the West Indies and Azores, p. 326, 1917).

*Upper Cretaceous Flora*.—The late Cretaceous and early Tertiary floras of New Zealand are known only from the determinations of Ettingshausen, whose identifications have not been generally accepted. Many of the plants were referred to northern genera, one was compared with a Greenland species, and the conclusion arrived at that the Tertiary flora of New Zealand was a part of that universal original flora from which all living floras of the globe descend. Ettingshausen supposed that from one part of the Tertiary flora of New Zealand the present flora was descended, while the other portion became extinct. Probably he has erred on the side of referring too many of the plants to northern genera, though there is nothing inherently improbable in supposing that the first dicotyledonous flora soon became widely distributed, and that the modern floras have differentiated from and displaced it. But such a universal flora would be Mesozoic, not Tertiary.

Ettingshausen referred the Shag Point and related plant beds to the Tertiary, while the Nelson and Westland series (Pakawau, Wangapeka, Reefton, and Grey River) was classed as Cretaceous. This order is now generally reversed. I am indebted to Mr. P. G. Morgan, Director of the New Zealand Geographical Survey, for kindly supplying me with information as to the relative ages of the principal New Zealand plant beds.

Omitting those identifications not founded on leaves, it may be profitable to analyse in a general way the floras described by Ettingshausen. Those which may be considered as of late Cretaceous age consist of 35 species from Shag Point, besides a few from Malvern Hills, Paparoa, Redcliffe Gully, and Murderer's Creek. Of the plants from Shag Point there are two ferns, one of which, said by Ettingshausen to occur also at Dunstan, a mid-Tertiary locality, may be compared with the recent *Dryopteris pennigera*. The gymnosperms comprise two species of *Agathis*, two of *Araucaria*, three of four podocarps and *Sequoia Novæ-Zealandiæ*. Judging by both the present and Tertiary distribution of these genera, northern relationships are indicated. The dictoyledons include eight species with simple entire leaves, a type characteristic of the existing flora. Three species referred to *Ficus*, *Hedycarya*, and *Cinnamomum* respectively likewise indicate an alliance with the north. In addition to these there are eleven species having serrated pinnately-veined leaves and two with palmate leaves. These are mainly referred to the Cupuliferæ, Myricaceæ, and Ulmaceæ, families which, except for *Nothofagus*, are scarcely characteristic of the present flora. Nothing can be said with any degree of certainty regarding the relationships of these plants, but if Ettingshausen's determinations have any value, they would support the evidence of the gymnosperms for a land connection towards the north. Such a connection would have been during Cretaceous times.

*Eocene Flora.*—The plants referred to the Cretaceous period by Ettingshausen are in reality of later date than the Shag Point fossils, and probably should be classed as Eocene. They consist of leaf and other impressions from the Nelson and Westland districts (Pakawau, Wangapeka, Reefton, Grey River). Four species of ferns are described, of which *Gleichenia obscura* and *Blechnum priscum* show relationships to recent tropical species. A fan palm named *Flabellaria sublongirachis* was present. The gymnosperms consist of *Ginkgocladus Novæ-Zealandiæ*, a relation of *Phyllocladus*; *Dammara Mantelli*, scarcely distinguishable from *Agathis australis*; and six of the appearance of podocarps, a group well represented in the living flora of New Zealand. The ferns and gymnosperms, therefore, show unmistakable evidence of relationships with the Malayan element of the New Zealand flora. The dicotyledons include five species with simple entire leaves and five with serrated leaves. These simple leaves are quite characteristic of the present flora of New Zealand. Two leaves named *Ficus similis* and *Cinnamomum Haastii* belong to types not now found in New Zealand, though, as *Ficus* and *Cryptocarya*, reaching Lord Howe Island. Besides these there are eight species referred to the Cupuliferæ and Ulmaceæ.

As in the late Cretaceous flora, the evidence of the dicotyledons for determining relationships is inconclusive. The gymnosperms, however, by the absence of *Araucaria* and the presence of *Dammara Mantelli, Ginkgocladus Novæ-Zealandiæ, Podocarpium prædacrydioides*, and *Dacrydium cupressinum* show closer relationships with the existing flora of New Zealand, and indicate the same alliances. Whether Tertiary or present gymnospermous floras be compared, therefore, the result is the same—namely, a former northern land extension is proclaimed.

The Tertiary flora of Seymour Island, held by Dusen to be Oligocene, contains the genera *Laurelia*, *Drimys*, *Knightia, Nothofagus*, and *Araucaria.* In all these, except *Knightia*, the relationship of the species is with South America. If correctly determined, the leaf referred to *Knightia* is of considerable interest.

*Palæozealandic Genera.*—Characteristic of New Zealand are many genera and family groups so distinct from any known elsewhere, yet taken together obviously descended from animals and plants that must have existed at a period when there was land connection between the New Zealand area and some other land mass, that they indicate a long period since the connection was severed. The last date that New Zealand formed part of this continent may be taken as some time in the Cretaceous period. It cannot have been later, otherwise land mammals would have entered the New Zealand portion. Cockayne's term Palæozealandic (Veg. N.Z. p. 315, 1921) might be applied to the genera here listed. His group is of mixed origin according to my views, some of the genera having arisen from the original continental flora, others from species that have afterwards come overseas.

The continental genera I include under the general heading Malayan element, because they represent the earliest of the higher animals and plants to people the New Zealand area, which I believe would be washed by the ocean except towards the north-west, and in their broader affinities may in most cases be compared with groups of northern origin.

The difference between northern and southern distribution is not so well marked with birds as with plants.

| NORTHERN DISTRIBUTION. | SOUTHERN DISTRIBUTION. |
|---|---|
| (a) *Genera with no near relations.* | |
| Plants. | Plants. |
| *Entelea, Melicytus, Alectryon, Astelia, Ixerba, Dactylanthus, Alseuosmia.* | *Corallospartium, Notospartium, Chordospartium, Carmichaelia, Anisotome, Aciphylla, Coxella, Pachycladon, Nothothlaspi, Stilbocarpa, Myosotidium, Celmisia, Haastia, Leucogenes, Phormium, Hoheria, Raoulia, Pseudopanax, Simplicia, Psychrophyton, Pleurophyllum.* |
| Birds. | Birds. |
| *Heterolocha, Callæas, Creadion, Turnagra.* | *Bowdleria, Nesolimnas, Cabalus, Notornis, Diaphoropteryx, Apteryx, Dinornithidæ, Xenicus, Traversia, Acanthositta, Nesonetta.* |
| Mammals—*Mystacops.*<br>Reptiles—*Sphenodon.*<br>Batrachia—*Liopelma.* | |
| (b) *Genera whose relationships are with Malaya and New Caledonia.* | |
| Plants. | Plants. |
| *Rhabdothamnus, Gymnelæa, Carpodetus, Knightia.* | *Siphonidium, Hebe, Coprosma, Pygmæa, Chrysobactron.* |
| Birds. | Birds. |
| *Hemiphaga.* | *Nestor, Gallirallus.* |
| (c) *Genera whose relationships are with Australia.* | |
| Birds. | Birds. |
| *Miro, Notomystis, Prosthemadera.* | *Sceloglaux, Myiomoira, Anthornis, Strigops.* |
| (d) *Genera whose relationships are with Amrrica.* | |
| Plants. | Plants. |
| *Corokia, Loxsoma.* | *Hectorella.* |

*The New Zealand Continent.*—Perhaps the outstanding feature of these lists is the large number of genera, including many with a large number of species, with a southern distribution. I take this as indicating a former considerable extension of land about and to the south of South Island, but not necessarily connected with the Antarctic Continent. The date can only be conjectured, but it may be put down as one of the periods when, judging by the geological history of New Zealand, there was a general uplift, perhaps in the Cretaceous and Eocene and again in the late Pliocene periods.

Two biological considerations indicate the continental character of the land. First, there is great diversity of species in the southern genera, species with their areas of distribution overlapping. Dinornithidæ, *Apteryx*, *Gallirallus*, *Hebe*, *Coprosma*, *Carmichaelia*, *Aciphylla*, *Raoulia*, *Celmisia*, and *Anisotome* may be mentioned. The crowding together of these species suggests a former wider area where they differentiated. As the land area diminished they have come together, so that many allied species are found in the locality. Willis interprets these facts as a southern invasion taking place later than a northern one (Ann. Bot. vol. xxxiii. p. 40, 1919). Where this so-called invasion came from we are not told.

Secondly, there are xerophytic characters in many New Zealand plants either in their whole life-history or during a portion of it, in a climate in which at present one would expect only mesophytes. Diels appears to have been the first to suggest that a continental extension was necessary to explain the presence of xerophyte plants in New Zealand, while Cockayne explains the developmental stages of many plants on the same assumption.

As these modifications affect entire genera, it must be presumed that the continental extension which induced their development was at the period when these genera were differentiated. That is, it must be placed early in the Tertiary period, and may therefore be mentioned in connection with the multiplication of species referred to the same cause.

On account of the many lines of evidence, both geological and biological, pointing to a former New Zealand continent, it has been accepted by geologists and biologists alike. The controversial points concern the area it occupied, the time it existed, and the lands it joined. The extension of land above indicated with a northern connection would evidently be sufficient to explain the Malayan basis of the New Zealand fauna and flora and the diversity of life now crowded in a comparatively small area. The early New Zealand continent would be a centre for the development and dispersal of many of the forms of life so characteristic of southern regions, including much of the so-called "Antarctic" flora and fauna. The penguins, shags, and petrels among birds, the Galaxiadæ among fish, the Geotridæ, and perhaps some marine molluscs, other invertebrates and algæ characteristic of southern regions and whose headquarters are in New Zealand, owe their development and distribution to the New Zealand continent, which in former times stretched towards Antarctica, the shore of which would act as a route for dispersal. The only other continent in the same latitude was South America. Australia and Tasmania since the Jurassic period do not appear to have extended much farther south than at present.

*Endemic Species of Malayan and Australian Genera.*—Beside the genera already mentioned there are in New Zealand representatives of many genera which show their greatest area of development in the Malayan region. The species in New Zealand belonging to these genera are all endemic, and their ancestors would enter by the northern land bridge described above. They would, in fact, be the last to enter by such a way. Hence the distribution of these species in New Zealand is for the most part northern.

The principal genera of Angiosperms in the New Zealand flora coming under the present heading are the following :—*Aristotelia*, *Drapetes*, *Coriaria*, *Edwardsia*, *Bagnisia*, *Nothopanax*, *Hedycarya*, *Melicope*, *Litsæa*, *Beilschmiedia*, *Weinmannia*, *Corynocarpus*, *Meryta*, *Schefflera*, *Gaultheria*, *Pratia*, *Paratrophis*, and *Metrosideros*. I cannot name any birds coming under the present heading; perhaps they change at a quicker rate than do plants. Certain land molluscs, however, such as *Placostylus*, *Rhytida*, and *Paryphanta* may be mentioned here.

Among genera characteristically Australian are some which possibly indicate migration over a continuous land surface. These may have entered by way of Northern Australia, New Caledonia, and Lord Howe Island. The following genera have species in one or more of these places:—*Olearia*, *Dracophyllum*, *Hymenanthera*, *Pennantia*, *Exocarpus*, and *Rhipogonum*. Three genera, *Fusanus*, *Quintinia*, and *Ackama*, are confined to the north of New Zealand, while *Plagianthus* is found in the south as well. Thus the Malayan land connection may explain the presence in New Zealand of Australian genera with all endemic species in New Zealand. That such genera as *Dracophyllum* and *Olearia* have been in the New Zealand area a long time is indicated by the large number of species belonging to each in New Zealand and their mainly southern distribution.

3. **The Influence of Antarctica.**—Perhaps no point concerning the origin and distribution of the New Zealand fauna and flora has given rise to more controversy than the so-called "Antarctic" element. This appears to me to be a mixture of several elements which are considered in different places in this paper. From the genera and species of plants common to New Zealand and South America I have first eliminated those which may be explained by migration from the north overland and from the west overseas. But there remains a residue which seem to demand a more direct land route between New Zealand and South America. By most authorities a land bridge is considered necessary. Thus Hutton, Benham, Chilton, and Cockayne in New Zealand and Hedley in Australia favour a continental connection. Cheeseman, Schucher, and Schenck, however, on the evidence of the flora think a closer approach of the land areas sufficient.

On account of the relatively small proportion of the New Zealand flora with "Antarctic" affinities and the larger Malayan element, also the contour of the ocean bottom and physical conditions of the Antarctic continent, it seems safe to assume that the most active period of transfer between the South American and New Zealand floras and faunas must have been at the time of New Zealand's greatest extension in late Mesozoic or early Tertiary times.

The genera of plants which, judging from their present distribution, have their greatest development in South America, and therefore are presumed to have supplied thence the New Zealand representatives, are *Griselinia*, *Ourisia*, *Discaria*, and *Gaya* with a predominantly southern distribution in New Zealand, and *Fuchsia*, *Jovellana*, *Laurelia*, *Phrygilanthus*, and *Muehlenbeckia* with a more northern or general distribution.

Unfortunately there is nothing known of the early Tertiary Antarctic flora beyond a few Oligocene plants from Graham Land. These are in the main South American types. However, if they are to be taken as an indication of the flora of the Antarctic coast at that time, then it is evident that New Zealand received no more of it than fragments that might have crossed, with the assistance of birds or wind, a small expanse of ocean.

*Griselinia* has four species in Chile and two in New Zealand, the latter species being different in appearance and perhaps belonging to a distinct section of the genus.

*Ourisia* has 19 species in South America, eight in New Zealand, and one in Tasmania. They are mainly plants of mountainous districts, where opportunities for dispersal and establishment are frequent.

*Discaria* has about 18 species in extra-tropical and Andine South America, one in Australia, and one in New Zealand. The two last are closely allied, and *D. discolor* of South America is related to *D. toumatou* of New Zealand.

The New Zealand species of *Gaya* has much larger flowers than any of the 10 South American species.

*Fuchsia* has about 60 species in America from Mexico and Fuegia. Of the three New Zealand species two are closely allied, and the third is local in the northern portion of the Dominion.

Neither of the two species of *Jovellana* in New Zealand is generally distributed. There are two or more species in Chile and Peru.

*Laurelia* has two species in South Chile and one in New Zealand. An extinct species has been described from the Oligocene of Graham Land. The genus is nearly allied to the Australian *Atherosperma*.

*Phrygilanthus* has about 20 species in South America, four in Australia, and two in New Zealand (both rare).

*Muehlenbeckia* has 10 species in South America, seven in Australia (one extending to New Zealand), four others in New Zealand, and one in the Solomon Islands. Of the New Zealand species three are mainly coastal and another occurs in mountain localities.

The species above mentioned show a certain amount of distinctness from the related South American forms, thus indicating the lapse of a long period of time since dispersal took place. They might well be the descendants of stray immigrants that crossed the sea that separated the late Mesozoic or early Tertiary New Zealand continent from Antarctica.

Besides the genera listed above which indicate the derivation of New Zealand species from a South American source, there are a few others which point to migration in the opposite direction.

*Dacrydium*, a genus probably of Malayan origin with its present greatest development in New Zealand, has in Chile a single species, *D. Fonckii*,* related to *D. laxifolium* of New Zealand.

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* Hutchinson (Kew Bulletin, 1924, p. 54) omits Chile in giving the range of *Dacrydium*.

*Pseudopanax* has five species in New Zealand and two in South Chile.

Perhaps bicentric genera like *Uncinia*, and *Gunnera* with the subgenus *Milligania* confined to New Zealand and Tasmania, and the closely-related subgenus *Misandra* to Chile, Fuegia, and the Falkland Islands, owe their distribution to the former presence of a habitable Antarctic continent.

Discussing the distribution of *Uncinia*, Guppy ('Plants, Seeds, and Currents in the West Indies and Azores,' p. 501, 1917) comes to the conclusion that whilst South America was the original differentiating ground of the genus, New Zealand with a single section has been in later times more vigorous and productive of species. The same author, however (p. 328), thinks that Antarctica has not shared in the history of the plant world since the appearance of Dicotyledons.

The genera enumerated in the preceding paragraphs must be taken as indicating at least an approximation of the New Zealand area to that of Antarctica at some time in the past. It is known that Graham Land supported a land flora as late as the Oligocene period—that is, long after Dicotyledons appeared. But a direct land connection does not appear to be necessary, because of their fragmentary nature and, as has already been pointed out, the species now common to South America and New Zealand form a disharmonic community.

There does not exist in New Zealand a plant association related to any in South America, all dominant plant species in New Zealand, including *Nothofagus*, being of northern derivation. It may be pointed out too that both the Tertiary, so far as is known, and the recent floras of New Zealand and South America are fundamentally different. The views herein expressed coincide almost exactly with those of Cheeseman (Rep. Aust .Ant. Exp., Bot. vol. vii. pt. 3, p. 53).

*South American–Tasmanian Biological Relations.*—The relationship of the flora of Tasmania to that of South America is far less than that of New Zealand to South America. The New Zealand continent, indeed, seems to have been the source of such plants in the Tasmanian flora as *Aciphylla, Psychrophyton*, and *Schizeleima*, and, if so, probably that portion of the South American element in the Tasmanian flora represented by *Gunnera* and *Ourisia* was received by way of the New Zealand continent.

The South American element in the Tasmanian flora is apparently quite small, and that portion which it has not also in common with New Zealand might be explained by drift from the Antarctic continent when its shore supported vegetation and the land extended from Australia to the south of Tasmania.

*Lomatia* has three species in Chile, four are described from the Oligocene of Graham Land, and there are six existing species in Tasmania and Eastern Australia.

*Embothrium* has four species in South America and one in Eastern Australia. *Eucryphia* has two species in Chile, one in Tasmania, and one in New South Wales. *Prionites* has one species in Fuegia and one in Tasmania. On the other hand, two Chilean species belonging to the genera *Fitzroya* (allied to *Diselma*) and *Orites* may indicate drift from the Tasmanian land extension to the Antarctic shore-line.

Much has been made in the past of the relationship of the mammals of South America and Australia, but it has been shown that the South American *Prothylacinus* is a creodont, and that the so-called Diprotodonts of South America are not to be included with the true Australian Diprotodonts, but are in reality a distinct group descended from American Polyprotodonts. Likewise the reptile from the South American Tertiary supposed to be near the Australian *Miolania* has been shown to be quite distinct (Regan, Terra Nova Exp., Zool. vol. i. pt. 1, p. 41, 1914). Finally, Dunn (Amer. Naturalist, vol. lvii. p. 135, 1923) has pointed out that all Amphibian distribution can be explained without recourse to land bridges save connections in the north between the northern land masses.

**4. Species Dispersing Overseas.** *Species dispersing from Australia to New Zealand.* (a) *Endemic New Zealand genera.*—The constant arrival of species of Australian plants in New Zealand overseas during the Tertiary epoch would result in different degrees of endemism according to the time since the species established themselves in New Zealand. Species arriving early and not subject to later additions might become so different as to be classed as distinct genera, others might differentiate into distinct species, but those species that were constantly dispersing individuals to New Zealand or which arrived recently would be identical with Australian ones.

These conditions would result if during past ages there had been a steady easterly movement, including chance arrivals and regular migrants, of plants across the Tasman Sea. The first degree of endemism by which there result in New Zealand distinct genera derived from Australian species may be represented by *Oreostylidium*, *Phyllachne*, *Colensoa*, *Hydatella*, *Sporodanthus*, and *Oreobolus*. Of these, *Phyllachne* and *Oreobolus* have supplied species farther eastward to South America.

(b) *Australian genera with endemic species in New Zealand.*—(1) PLANTS. Included here are a number of fairly large Australian genera with one or few species in New Zealand all or some of which are endemic. The following genera have each one endemic species in New Zealand, the remainder of the species being Australian: *Phebalium* (27 species in Australia), *Epacris* (23), *Persoonia* (60), *Myoporum* (25), *Swainsonia* (32), and *Logania* (18).

*Pimelia* has 80 species in Australia and 12 in New Zealand. They are mostly plants of the coast and mountain scrub. *Haloragis* has 41 species in Australia and Tasmania, of which four extend to New Zealand, and there is an endemic species in New Zealand as well. *Leptospermum* has 25 species in Australia and three in New Zealand (one of which is Australian). *Centrolepis* has 18 species in Australia, one in New Guinea, and two in New Zealand (one of which is Australian). Other Australian genera with a few species in New Zealand are *Pomaderris*, *Brachycome*, *Cyathodes*, and *Leucopogon.* Smaller genera that may be mentioned here are *Arthropodium, Poranthera, Archeria,* and *Forstera.*

In all the above genera, the New Zealand species, judging from the small number represented, may be assumed to be descendants of chance arrivals.

In some cases the distribution suggests that Australian genera supply species to South America direct or by way of New Zealand. Thus *Pratia,* a genus with its headquarters in Australia, but extending to New Guinea and the Himalayas, has three species in New Zealand and one in South America. *Lagenophora* has four species in Australia and Tasmania, six in New Zealand, two in Polynesia, and four in South America. *Abrotanella* is very similar in distribution, having three species in Tasmania and Victoria, one in New Guinea, seven in New Zealand, three in South America, and one in Rodriguez. *Haloragis erecta* extends to Juan Fernandez. This type of distribution is also shared by the South African genus *Leptocarpus*, which has 11 species in Australia, one in New Zealand, and one in South America.

(2) BIRDS. There are three species of New Zealand birds which seem referable to the category of endemic species differentiated from Australian arrivals—namely, *Coturnix novæ-zealandiæ*, *Casarca variegata,* and *Anthus novæ-zealandiæ.* All are birds of the open country.

(c) *Species identical in Australia and New Zealand*: *Plants.*—The species of plants common to Australia and New Zealand may be considered in groups according to their distribution beyond these two countries.

It is not contended here that the explanation of the presence in New Zealand of all the species mentioned in the following paragraphs is due to their having migrated from Australia across the Tasman Sea. But it is suggested, that on account of their existing as identical species in the two regions which have been separated during the greater portion of the Tertiary period, and the general eastward movement of plants in the South Temperate Region, the probability is that the bulk of them have made the passage overseas and in the direction west to east.

(1) Cosmopolitan species are here defined as those which extend to the continents of both the Eastern and Western Hemispheres. Besides 19 species of pteridophytes there are in New Zealand 61 flowering plants of this nature. They consist of 24 grasses, sedges and rushes, five composites, 12 coastal plants, 12 freshwater plants, and eight others (all herbs). It is evident that all these species owe their wide distribution to means of or opportunities for dispersal. To say that they are all or mainly old species as one might infer from Willis's 'Age and Area' hypothesis gives no satisfactory explanation. When independent evidence of the age of these species is forthcoming it should prove or disprove Willis's theory.

(2) There are a number of species (I have listed 25 of flowering plants) which are distributed over Australia, Tasmania, portions of Malaya, Polynesia, and New Zealand, but do not extend to South America. Half of them are grasses and sedges, the remainder herbaceous plants of the coast, fresh water, scrub, or mountain. Forty species of pteridophytes belong to this group, including *Todea barbara*, found only in South Africa, Australia, Tasmania, and New Zealand.

(3) About 12 species of flowering plants and nine pteridophytes have a southern distribution that would suggest Australia as a starting point, distributing thence to New Zealand and South America. They are of the same general nature as those already mentioned, as far as means and opportunities for dispersal are concerned. They include *Haloragis erecta*, *Myriophyllum elatinoides*, *Geranium sessiliflorum*, *Selliera radicans*, *Gratiola peruviana*, *Carex pumila*, and *Juncus planifolius*. Two species, *Mesembryanthemum æquilaterale* and *Tetragonia expansa*, have their distribution, in addition to the countries mentioned, recorded as California and Japan respectively, while three have apparently continued their easterly route beyond South America, *Nertera depressa* reaching Tristan d'Acunha, and *Scirpus nodosus* and *Apium prostratum* South Africa.

(4) There are 135 species of flowering plants and 19 pteridophytes confined to Australia, Tasmania, and New Zealand. The flowering plants may be classed under the following systematic and ecological groups:—Grasses, 18 species; sedges and rushes, 19; orchids, 15; composites, 9; coastal plants, 11; swamp and other freshwater plants, 23; scrub plants, 20 (of which five are woody); mountain plants, 14 (of which four are woody); forest plants, six (five herbs and *Pomaderris apetala*). This list may be compared with that of the Kermadecs previously mentioned. It has, in fact, the characteristics of the flora of an oceanic island. The inference is that these plants might have crossed the Tasman Sea between Australia and New Zealand by occasional means of transport. A few of them are quite rare in New Zealand.

The New Zealand orchids are mainly of Australian affinity. Of the genera, 14 (including 39 species) may be described as Australian, whilst seven (including 17 species) are mainly Malayan. This distribution would suggest that the family reached its highest development after the connection between New Zealand and the North was severed, and the species found their way by wind carriage; hence the preponderance of Australian forms.

The characteristics of the 320 plants common to New Zealand and Australia have already been indicated. They are plants of the shore, lake, swamp, scrub, grassland, and mountain. Taken as a whole they correspond with the type of flora found on oceanic islands, and therefore do not require the hypothesis of a land connection with Australia to explain their presence in New Zealand. In each country those large genera which stamp the flora as distinct from that of other lands and form the bulk of the forest vegetation have few or no representatives common to the two countries. The plants which are common give no indication whatever of any migration as a whole flora from one country to another.

*Birds.*—There are three species of land birds common to Australia and New Zealand: *Ninox novæ-zealandiæ*, *Rhipidura flabellifera*, and *Zosterops lateralis*. Of these the last appears to have found its way from Tasmania since New Zealand was settled by Europeans, it having been first noted in the south-west of Otago in 1832. Of birds listed as stragglers—that is, those which have been recorded in New Zealand from a few specimens presumably carried accidentally by storms—there are about 40 species, not counting petrels. They include two land birds (*Graucalus robustus* and *Coleia carunculata*) and seven species of rails and herons, which are inhabitants of fresh water. To these may be added three species of ducks. These last nine species are of interest as indicating how seeds of water plants, grasses, and sedges might be transported. The Grey Duck (*Anas superciliosa*) wanders far; it and the Harrier (*Circus approximans*) are regular visitors to Sunday Island, 600 miles to the north-east of New Zealand.

*Species dispersing from South America to Tasmania and Australia.*—That there is a continuous stream of migrants originating in South America and moving eastwards is a conclusion that seems evident from the facts of distribution of the plants of the southern portions of Chile and Patagonia. Most of them, one must assume, perish at sea, many reach the Falklands, fewer South Georgia, still fewer the islands of the South Indian Ocean, some Tasmania, and more New Zealand and the islands to the south. It appears to be a question of latitude and distance. Thus the islands closest to South America are most favoured by these Fuegian plants, whilst of those farthest away the more southern, as the South Island of New Zealand, receive more than those such as Tasmania, which lie slightly farther to the north. Certain South American genera have their farthest eastward range in Tasmania—*Eucryphia*, *Prionites*, and *Acæna* section *Acrobyssinoides*. Others occur in New Zealand as well. Such are *Pernettya* (20 in South America, one in Tasmania, one in New Zealand), *Gentiana* section *Andicola* (50 in South America, one in Tasmania, one in New Zealand), and *Oreomyrrhis*.

*Species dispersing from South America to New Zealand.*—Three Fuegian species of flowering plants are, in the New Zealand region, found only on the islands of the route and east. *Rostkovia magellanica* and *Azorella Selago* have shown their route and origin by their occurrence on intermediate islands, but *Carex Darwinii* outside South America has been found only in the Chatham Islands. Besides these a fern (*Polystichum mohrioides*) is found at the Auckland Islands.

A class of plants not far removed from these so far as distribution is concerned is that consisting of those species occurring in South America, the Subantarctic Islands and mainland of New Zealand, and sometimes intermediate islands. Such are *Cardamine glacialis*, *Tillæa moschata*, *Carex trifida*, and *Ranunculus acaulis*.

Just as there are New Zealand genera of plants having representatives in South America, so there are South American genera or sections of genera with species in New Zealand. They are fewer, however, and more southern in their New Zealand distribution. Besides those already mentioned as occurring also in Tasmania, there are *Enargea*, *Marsippospermum*, *Carex* sections *Bractiosæ* and *Aciculares*, *Geranium* sections *Chilensia* and *Andina*, *Acæna* section *Euancistrum*, and *Caltha* section *Psychrophylla*. *Colobanthus* is a genus whose species appear still to be dispersing both from South America and New Zealand. There are 10 species in Andine South America, the Falklands, South Georgia, and Graham Land (*C. crassifolius*). Two of these are found in New Zealand. There are nine species in New Zealand, one in Kerguelen, another in New Amsterdam Island, and a third in Victoria and Tasmania.

*Species dispersing from South Africa.*—It is not here contended that any species have arrived in New Zealand direct from South Africa, but there are several genera which have their centre of dispersal in South Africa and which extend eastward through Australia to New Zealand. Such are *Leptocarpus*, *Hypolæna*, *Hypoxis*, *Wahlenbergia*, *Tetragonia*, and *Mesembryanthemum*.

*Species dispersing from Polynesia to New Zealand.*—A few species of New Zealand plants may be regarded as having been derived from Polynesia by trans-oceanic migration. *Dianella intermedia*, *Peperomia Urvilliana*, *Macropiper excelsum*, *Pisonia Brunoniana*, and the ferns *Diplazium japonicum*, *Hymenophyllum demissum*, *H. dilatatum*, and *Dryopteris Thelypteris* are suggested as coming under the present heading, while the orchids of the genera *Earina*, *Dendrobium*, *Bulbophyllum*, *Gastrodia*, and *Corysanthes* may be descendants of Polynesian immigrants. *Ascarina* is a genus of forest trees that seems capable of crossing wide expanses of ocean. There are three species in New Caledonia and one each in the Philippines, Fiji, Samoa, Tahiti, Raratonga, Kermadecs, and New Zealand. The species from the Kermadecs, Fiji, Samoa, and Raratonga are very closely allied, and related to *A. lucida* of New Zealand.

*Species dispersing from New Zealand to Australia and Tasmania.*—The number of genera having many representatives in New Zealand and with few species in Australia and Tasmania is small compared with those large Australian genera which have one or few species in New Zealand. Furthermore, in the case of the New Zealand genera herein mentioned, the species in Tasmania and Australia are all endemic, showing that transport is quite occasional, if indeed it was not confined to the period when the New Zealand continent extended towards Tasmania. The following New Zealand genera are considered to have distributed species overseas to westward: *Gunnera* subgenus *Milligania* (nine species in New Zealand, one in Tasmania); *Azorella*, sect. *Schizeleima* (nine in New Zealand, one in Australia, two in South America); *Ourisia* (19 in South America, eight in New Zealand, one in Tasmania); *Aciphylla* (14 in New Zealand, four in Tasmania and Australia); *Celmisia* (43 in New Zealand, one in S.E. Australia); *Psychrophyton* (seven in New Zealand, one in Tasmania); *Hebe* (90 in New Zealand, two in Tasmania and Eastern Australia). In nearly all the above-mentioned cases the species are mountain plants, and the range on the western side of the Tasman Sea is Tasmania and South-East Australia.

*Species dispersing from New Zealand to Polynesia.*—There are a few genera of Angiosperms whose centre of dispersal is apparently New Zealand and which have one or two species in the Pacific Islands. *Astelia* has one species in Fiji and Samoa, two in the Hawaiian Islands, and one in Tahiti. There is a species of *Oreobolus* recorded from the Hawaiian Islands. *Coprosma* occurs in several islands of the Pacific, as far as Hawaii and Tahiti. *Melicytus ramiflorus* is found in Norfolk Island, the Kermadecs, Eua (Tonga Group), and Fiji. *Coriaria ruscifolia* has reached the Kermadecs, Banks Islands, Fiji, Samoa, Tahiti, and South America; whilst *Edwardsia microphylla* occurs in Easter Island, Juan Fernandez, South America, and Gough Island. There are also three species of ferns widely distributed in New Zealand but only known elsewhere from one island in the Pacific; they are *Lomaria filiformis* and *Polystichum Richardi* in Fiji and *Polypodium dictyopteris* in New Hebrides.

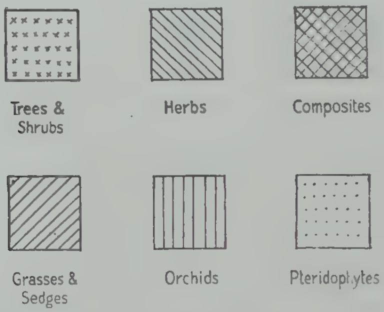
*Species dispersing from New Zealand to South America.*—In considering the origin of the New Zealand element in the South American flora we may omit the ferns, and about 13 others which are cosmopolitan in their distribution, but take into account those species in South America which are closely allied to New Zealand species. The feature of these plants is that most of them belong to genera whose centre of dispersal is apparently New Zealand or Australia. And this fact, together with the oceanic character of the species, taken as a whole suggests trans-oceanic migration as the explanation of their present distribution.

Among Australian genera with species in South America identical or allied to species in New Zealand the following may be mentioned:—*Abrotanella*, the three South American species are related to New Zealand ones; *Gaimardia*, belonging to an Australian family, has one species in Tasmania, one in New Guinea—*G. setacea* in New Zealand and *G. australis* (allied to *G. setacea*) in Fuegia and the Falklands. *Lagenophora*, mainly Australian and New Zealand, has four species in Andine South America, one of which is closely related to *L. pumila* of New Zealand; *Pratia repens* in Chile, Fuegia, and the Falklands is related to the New Zealand *P. angulata*;

*Haloragis erecta* of Australia and New Zealand extends to Juan Fernandez; *Leptocarpus* has one species in South America; *Drosera* section *Psychrophylla* has one species in Tasmania, Australia, and New Zealand, another in New Zealand, and a third in Chile, Fuegia, and the Falklands.

The genera or sections of genera which may be considered of New Zealand origin and having one or a few species in South America are as follows:—*Hebe*, with about 90 species in New Zealand, has *H. elliptica* in the south of South America, Subantarctic Islands, Fuegia, Chile, and the Falklands; whilst *H. salicifolia* of New Zealand has an ally (*H. Fonckii*) in South America. *Coprosma* has one species (*H. triflora*) in Juan Fernandez; *Myosotis* is a North Temperate genus with 24 species in New Zealand, of which one extends to Patagonia and there is another, related to a New Zealand species, in Magellan; *Astelia*, whose centre of dispersal is New Zealand, has one species in Fuegia and the Falklands (*A. pumila*) related to *A. linearis* of New Zealand; *Schizeleima* (section), with nine species in New Zealand and one in Australia, has two in South America; some small genera with one or few species in New Zealand and one in South America should probably be classed here—*Tetrachondra, Phyllachne, Donatia.*

Fig. 6.



Explanation of signs used in Figs. 1–5.

There are a few genera which I class as of Malayan origin, but New Zealand is probably the centre from which the South American species have been derived. They are *Aristotelia, Nertera, Coriaria*, and *Edwardsia.*

Enough has now been given to show that the New Zealand region appears to have been a centre of dispersal for many species that reach as far eastward as South America, and that in their characteristics as regards means of dispersal and occupying habitats giving opportunities for dispersal and establishment, the plants common to New Zealand and South America compare with those found on an oceanic island. The conclusion seems to be inevitable that plants have been carried from New Zealand to South America by agencies comparable to those which populate the remote islands of Polynesia. Exactly what these agents are may require long and close observations in inhospitable climates.

*Circum-austral Species.*—As if showing that distribution is now actually taking place, there are several circum-austral species which, beginning in one of the southern land masses, have completed the circuit of the globe. Such are *Nertera depressa*, *Ranunculus biternatus*, *Tillæa moschata*, *Callitriche antarctica*, *Festuca erecta*, *Edwardsia microphylla*, *Scirpus nodosus*, *Apium prostratum*, *Agrostis magellanica*, *Crantzia lineata*. *Oreomyrrhis andicola*, and *Acæna adscendens*.

## VI. SUMMARY.

1. There has been a continuous land surface in the New Zealand area since the beginning of the Mesozoic epoch. The early Triassic period appears to have been a time when there was a direct land connection with the north. In the late Triassic a flora consisting of Equisetales, Filicales, and Ginkgoales was common to New Zealand and other southern lands. This flora, together with *Sphenodon*, *Liopelma*, and possibly *Peripatus*, would date from the time of the former northern land connection.

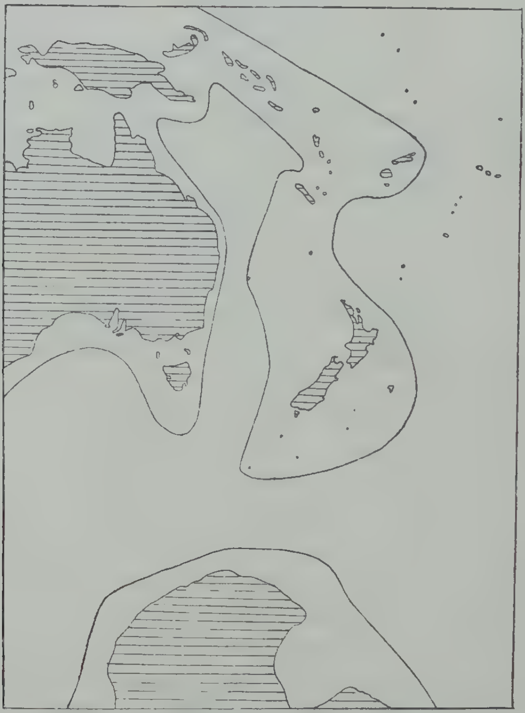
2. In the later Triassic and in the Jurassic periods there were times when the land was lower and a long series of marine sediments was laid down. Throughout this time there flourished on the land surface a flora including Filicales, Cycadofilices, *Podozamites*, and the early forms of Coniferales. The Jurassic flora was nearly uniform in character throughout the world, extending beyond the Arctic and Antarctic circles.

3. In Cretaceous times the land in the New Zealand area was of continental dimensions. It extended to the north so as to connect with New Guinea and North-Eastern Australia, but Western Australia was separated from this continent by an arm of the sea. A sea also intervened between the New Zealand area and Southern Australia (with Tasmania), but the land extended to the south and east so as to include the area of the submarine plateau on which now stands the Auckland, Campbell, Antipodes, and Chatham Islands. The Antarctic continent during this period of elevation no doubt extended farther to the north, approaching perhaps within a few hundred miles of the New Zealand continent. Possibly Macquarie Island was much larger than at present. Mr. H. Hamilton informs me that it contains altered sedimentary rocks of unknown age. According to Thomson (Rept. Austr. Ant. Exp., Zool. vol. iv. p. 60, 1918), the late Jurassic or early Cretaceous was a period of emergent lands all round the Pacific.

The map given by Hedley (Proc. Linn. Soc. N.S.W. vol. xxiv. p. 404, 1899) represents precisely what, judging from the present New Zealand flora and the evidence gradually accumulating of the flora of New Guinea and the islands of the western Pacific, I think necessary for a land connection in the Cretaceous period. The route taken by plants and animals migrating between New Zealand and the north is as clearly marked by the present distribution of *Agathis* and *Araucaria* as by that of *Placostylus*. The accompanying map, therefore, shows a former land bridge by way of Lord Howe Island, New Caledonia, and the New Hebrides, but I cannot follow Mr. Hedley in his Antarctic connections to the southward.

The Cretaceous period was important in the history of New Zealand, which afterwards was not again united with any other land. The period of land connection with the north must have lasted some time, for two continental floras succeeded one another in the New Zealand area. The first comprised the modern types of Coniferales and Filicales, and the more primitive Angiosperms such as *Nothofagus*. Such genera as *Araucaria, Libocedrus, Phyllocladus*, and *Nothofagus* appear to have arisen in North America and migrated along the western shore of the Pacific; hence their presence in Australia and New Zealand but absence from Africa. The second flora included the bulk of the ancestors of the Malayan element in the present flora. It included Angiosperms, and with it were associated birds, lizards, insects, and other animals.

Fig. 7.



Map of South-west Pacific showing greatest extension of land required for the dispersal of Spermophytes in late Mesozoic times.

Overseas came many animals and plants, some from Australia and Tasmania across the Tasman Sea, and a few from the shores of the Antarctic continent, which supported vegetation.

The New Zealand continent not only received but gave to neighbouring lands some of its productions. It was a centre for the development of many peculiar groups of plants and animals. Shut off from mammals which spread over the world in late Mesozoic and early Tertiary times, its birds filled their place, and a great variety of flightless forms—Dinornithidæ, *Apteryx*, rails —originated. In the same diversified and extensive land area the plants likewise increased and differentiated along lines adapted to different stations. Hence arose the many species of *Hebe*, *Coprosma*, *Celmisia*, *Olearia*, *Carmichaelia*, and others. It was in the southern portion of the continental area that this new world of life came into existence. Some of these forms wandered back along the land bridge to the north, as *Carmichaelia* and *Phormium*; a few found their way to the southern part of Australia and Tasmania, as *Aciphylla*, *Celmisia*, and *Psychrophyton*; while some even reached the shores of Antarctica, as *Pseudopanax* and perhaps *Dacrydium*.

4. On the breaking down of the land connection to the north the exchange of species between New Zealand and other countries was confined to such as could by chance cross a considerable stretch of ocean. Nevertheless, a great many species of plants both arrived and departed from New Zealand, the lands both receiving and giving being mainly those in the same latitudes—Australia, Tasmania, and South America. A small north and south movement between Polynesia and New Zealand also took place. But in accordance with the means of and opportunities for dispersal this moving population has the characteristics of the inhabitants of truly oceanic islands. The principal sections of the flora received since New Zealand severed its last direct land connection are the orchids and the Australian species.

The flora as it stands today I have endeavoured to represent by means of a diagram (fig. 1). Its derivation for the most part by direct land connection in the north, gives its forests which have nearly half of their species woody plants (some trees and shrubs are included in the Composites), and also a considerable proportion of woody species in the scrub and grassland formations. Continental conditions including diversified mountainous country are shown by the mountain plants equalling the forest plants (30 per cent. each). From Dr. Cockayne's work on the vegetation of New Zealand, I gather that he considers that the mountain plants were mainly differentiated in late Tertiary times. This may be so, but large distinct genera evidently require a longer period for their differentiation.

The paucity of orchids, so abundantly developed in New Guinea and New Caledonia, leads one to conclude that this family reached its highest development after New Zealand's connection with the north had been severed. Composites, which figure so largely in the New Zealand flora (14 per cent.), are mainly plants of the scrub and grassland areas. Their great development is perhaps a result of continental conditions in both early and late Tertiary times.

In the preparation of this paper I have endeavoured to group the plants and some of the animals of New Zealand according to their place of origin. For the facts of plant distribution I am especially indebted to the works of Cheeseman, Cockayne, and Skottsberg. The main groups of animals not dealt with—earthworms, insects, spiders, and crustacea—have all been used to support the theory of an Antarctic connection in late Mesozoic or early Tertiary times. But opinion is not unanimous on this point, and I venture to predict that, as methods of dispersal among the invertebrates are better known, the arguments for trans-oceanic migration will be strengthened.

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| | No. of Species. | | | | | | Percentages. | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coastal. | Freshwater. | Scrub and grassland. | Forest. | Mountain. | Totals. | Coastal. | Freshwater. | Scrub and gras land. | Forest. | Mountain. | Totals. |
| | *New Zealand and Stewart Island.* | | | | | | | | | | | |
| Trees and shrubs ........ | 25 | .. | 52 | 183 | 80 | 340 | 2 | .. | 4 | 13 | 6 | 25 |
| Herbs.................. | 56 | 70 | 92 | 59 | 174 | 451 | 4 | 5 | 6 | 4 | 12 | 31 |
| Composites ............ | 18 | 4 | 48 | 24 | 103 | 197 | 1 | .. | 4 | 2 | 7 | 14 |
| Grasses, sedges, and rushes. | 22 | 63 | 62 | 28 | 59 | 234 | 2 | 4 | 4 | 2 | 4 | 16 |
| Orchids ................ | .. | 5 | 17 | 28 | 5 | 55 | .. | .. | 1 | 2 | .. | 3 |
| Pteridophytes .......... | 3 | 8 | 32 | 97 | 6 | 146 | .. | 1 | 2 | 7 | 1 | 11 |
| | 124 | 150 | 303 | 419 | 427 | 1423 | 9 | 10 | 21 | 30 | 30 | 100 |
| | *Lord Howe Island.* | | | | | | | | | | | |
| Trees and shrubs ........ | 8 | .. | 5 | 49 | .. | 62 | 4 | .. | 2 | 24 | .. | 30 |
| Herbs.................. | 24 | 2 | 17 | 20 | .. | 63 | 12 | 1 | 8 | 10 | .. | 31 |
| Composites ............ | 3 | .. | 5 | 4 | .. | 12 | 1 | .. | 2 | 2 | .. | 5 |
| Grasses, sedges, and rushes. | 3 | 5 | 5 | 6 | .. | 19 | 1 | 2 | 2 | 3 | .. | 8 |
| Orchids ................ | .. | .. | 1 | 3 | | 4 | .. | .. | 1 | 1 | .. | 2 |
| Pteridophytes .......... | 1 | 1 | 4 | 43 | .. | 49 | 1 | 1 | 2 | 20 | .. | 24 |
| | 39 | 8 | 37 | 125 | .. | 209 | 19 | 4 | 17 | 60 | .. | 100 |
| | *Kermadec Islands.* | | | | | | | | | | | |
| Trees and shrubs ........ | 3 | .. | 1 | 14 | .. | 18 | 3 | .. | 1 | 12 | .. | 16 |
| Herbs.................. | 17 | 2 | 8 | .. | .. | 27 | 15 | 2 | 7 | .. | .. | 24 |
| Composites ............ | 4 | .. | 4 | 1 | .. | 9 | 4 | .. | 4 | 1 | .. | 9 |
| Grasses, sedges, and rushes. | 8 | 6 | 4 | 2 | .. | 20 | 7 | 5 | 4 | 2 | .. | 18 |
| Orchids ................ | .. | .. | 1 | 1 | .. | 2 | .. | .. | 1 | 1 | .. | 2 |
| Pteridophytes .......... | 2 | 1 | 7 | 28 | .. | 38 | 2 | 1 | 6 | 24 | .. | 33 |
| | 34 | 9 | 25 | 46 | .. | 114 | 31 | 8 | 23 | 40 | .. | 102 |
| | *Australia—New Zealand.* | | | | | | | | | | | |
| Trees and shrubs ........ | 2 | .. | 5 | 1 | 4 | 12 | 1 | .. | 2 | .. | 1 | 4 |
| Herbs.................. | 29 | 40 | 26 | 8 | 11 | 114 | 9 | 13 | 8 | 3 | 3 | 36 |
| Composites ............ | 3 | 1 | 10 | 1 | 1 | 16 | 1 | .. | 3 | .. | .. | 4 |
| Grasses, sedges, and rushes. | 11 | 32 | 18 | 4 | 10 | 75 | 3 | 10 | 6 | 1 | 3 | 23 |
| Orchids ................ | .. | 3 | 12 | 1 | .. | 16 | .. | 1 | 4 | .. | .. | 5 |
| Pteridophytes .......... | 1 | 4 | 28 | 46 | 8 | 87 | .. | 1 | 9 | 15 | 3 | 28 |
| | 46 | 80 | 99 | 61 | 34 | 320 | 14 | 25 | 32 | 19 | 10 | 100 |
| | *New Zealand—South America.* | | | | | | | | | | | |
| Trees and shrubs ... .... | 1 | .. | 1 | 2 | .. | 4 | 1 | .. | 1 | 3 | .. | 5 |
| Herbs ................. | 8 | 10 | 4 | 3 | 5 | 30 | 12 | 15 | 6 | 4 | 7 | 44 |
| Composites ............ | .. | 1 | 1 | .. | 1 | 3 | .. | 1 | 1 | .. | 1 | 3 |
| Grasses, sedges, and rushes. | 2 | 8 | 3 | .. | 5 | 18 | 3 | 12 | 4 | .. | 7 | 26 |
| Orchids ................ | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Pteridophytes .......... | 1 | .. | 4 | 8 | 2 | 15 | 1 | .. | 6 | 12 | 3 | 22 |
| | 12 | 19 | 13 | 13 | 13 | 70 | 17 | 28 | 18 | 19 | 18 | 100 |

# On the Occurrence of Cavity Parenchyma and Tyloses in Ferns.

By H. S. Holden, D.Sc., F.L.S., University College, Nottingham.

(With 25 Text-figures.)

[Read 3rd April, 1924.]

The occurrence of cavity parenchyma in filicinean petioles is familiar to all students of fern anatomy, and there are a number of incidental references to its development in various genera and species scattered through the literature of the group. These references have been collected and amplified by Miss McNichol, who has also made a careful study of its development and maturation in a number of Polypodiaceæ and Cyatheaceæ, her results being published in the 'Annals of Botany' in 1908 [**7**]. Miss McNichol defines cavity parenchyma as "a special tissue formed by the conjunctive parenchyma cells of the vascular bundles of the petiole, which replaces the first-formed elements of the wood, sometimes by simply crushing the spiral vessels, but generally by means of tylose-like swellings within the cavity of the vessels." In the second case the formation of tylose-like swellings is followed by their subsequent enlargement, and results in the rupture of the protoxylem elements. Cavity parenchyma thus differs from true tyloses in the fact that its cells cause disruption of the xylem elements which they invade, and also in being confined to the protoxylem. Tyloses, as distinct from cavity parenchyma, are apparently very rare in existing Pteridophyta, and have been recorded only by Conwentz [**1**], who noted their occurrence in old petioles of *Cyathea insignis*. A second example recorded by Johnson [**4**] for *Pteridium aquilinum* is open to another interpretation, and will be referred to subsequently.

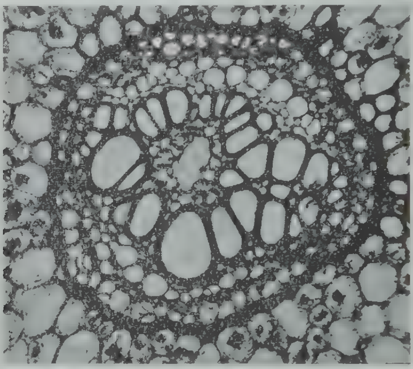
McNichol appears to regard cavity parenchyma as confined to the petiolar strands [**7**, p. 405], but there is little doubt that it is not uncommonly present in the rhizomes of certain species, this being notably the case in *Pteridium aquilinum*.

As a result of the examination of a considerable amount of material of *Pteridium* rhizome, the following conclusions appear to be reasonably well established:—

1. Cavity parenchyma occurs commonly but not invariably in the rhizomes of *Pteridium aquilinum*.
2. It is frequently well developed in the outer ring of meristeles and may involve the whole of these.
3. It is relatively rare in the inner meristeles and, where it does occur, is less strongly developed than in the outer meristeles.

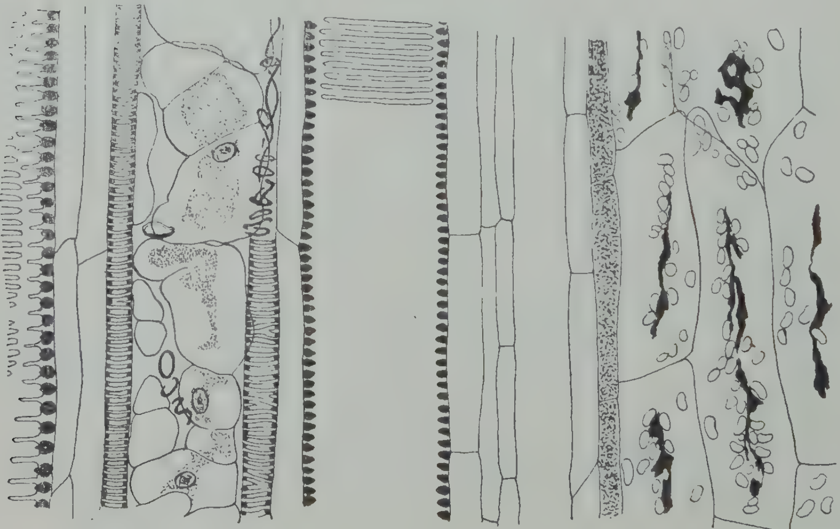
4. Its occurrence shows no evident relation to the proximity of the petiole traces, and cannot be regarded as due to an unusual downward continuation of the cavity parenchyma normally present in the petiole.

Fig. 1.



Photomicrograph of an outer meristele from the rhizome of *Pteridium aquilinum* in transverse section, showing cavity parenchyma replacing the mesarch protoxylem (× 400). From a negative by Professor W. H. Lang, F.R.S.

Fig. 2.

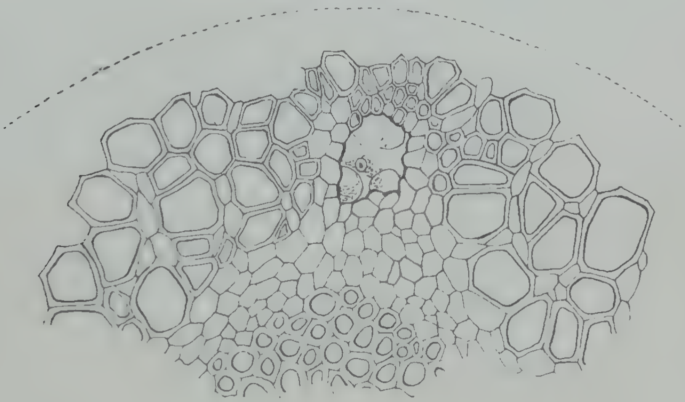


Longitudinal section of a portion of an outer meristele from the rhizome of *Pteridium aquilinum,* showing the cavity parenchyma and the disorganized remnants of the protoxylem (× 600).

Fig. 1 shows a typical example of its development in an outer rhizome bundle as seen in transverse section, whilst fig. 2 illustrates its characteristic features as seen in longitudinal section. The extremely irregular nature of the parenchymatous outgrowths and their disruptive effects on the protoxylem are very evident, so that it agrees exactly with that occurring generally in the petiole.

It is almost certain that the case of tylose formation recorded by Johnson [4] is in reality a case of cavity parenchyma formation. McNichol suggests that, in view of its being made from a small detached piece of material, "either it may have been made from a piece of petiole, the tylose-like cells being cavity parenchyma, or that, if cut from the rhizome, it represents an unusual case of continuation of the cavity parenchyma into the rhizome." There is nothing sufficiently characteristic in the tissues shown by Johnson's figures to enable one to identify the specimen with certainty as a rhizome, but, in view of the common development of cavity parenchyma in rhizome strands, his statement that the material was a rhizome may be accepted as correct.

FIG. 3.

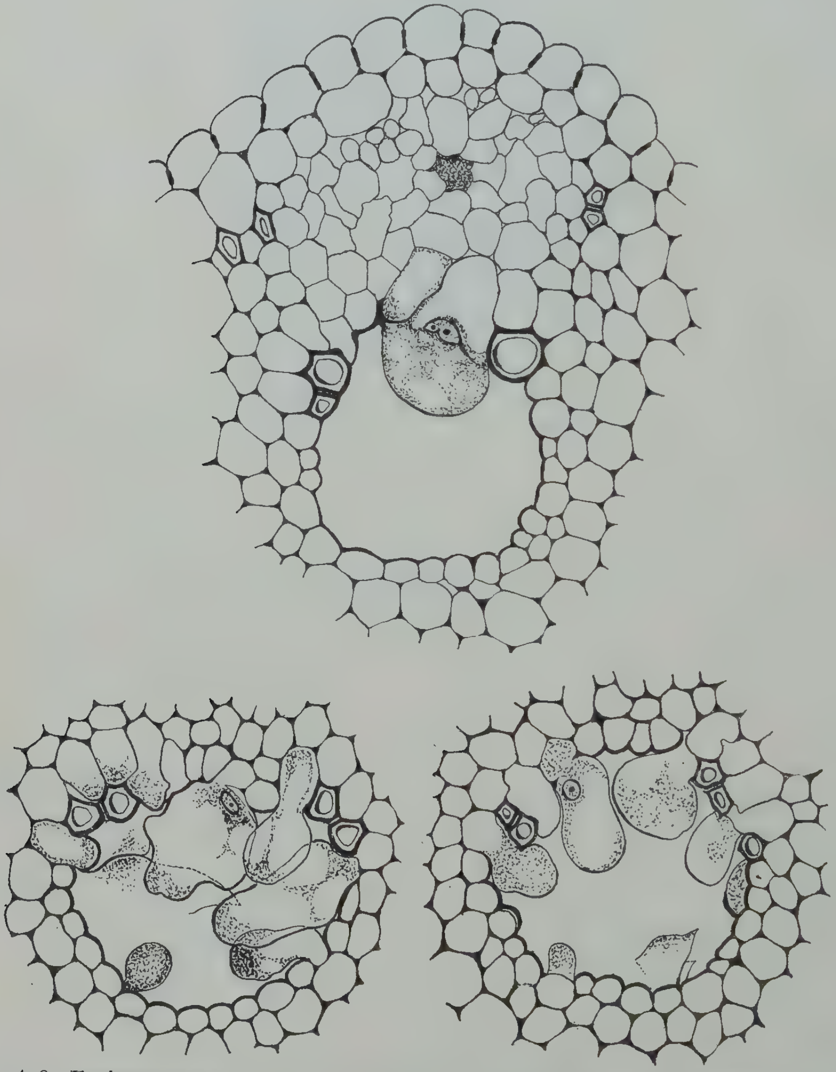


Portion of the outermost solenostele of *Matonia pectinata*, showing cavity parenchyma (× 400).

Although an examination of a number of other filicinean rhizomes has been made, only one additional case of cavity parenchyma formation has been discovered. This occurred in *Matonia pectinata* in a mature rhizome possessing three concentric solenosteles, only the outermost one of which was involved (fig. 3). The material from which the sections were obtained was a small fragment of rhizome forming part of the material brought by Tansley from the Malay States. In view of the fact that neither Seward [10] nor Tansley and Lulham [14] refer to the formation of cavity parenchyma in *Matonia pectinata,* it seems probable that its formation in this species is exceptional.

It is interesting to note that ingrowths essentially of the same type as cavity parenchyma may be present in *Equisetum.* Strasburger [12] indeed mentions the projection into the carinal canal of parenchymatous cells associated with the large connected masses of pitted nodal tracheids, and the same feature is discussed in a more recent paper by Sykes [**13**]. The case figured below (figs. 4–6) is, however, obviously of a somewhat different character. The specimen was one of *Equisetum arvense*, the aerial stem of which has been injured and had broken off below ground-level at its junction with the rhizome. Sections of the rhizome *internode* near the injury show that in addition to a localized browning of the cortical parenchyma and a partial

Figs. 4–6.



Figs. 4–6. *Equisetum arvense*—Transverse section of carinal canals of rhizome, showing varying degrees of occlusion by tylose-like ingrowths and the development of a cuticle on the cells lining the canal (× 400).

collapse of the phloem cells, there has been a development of parenchymatous ingrowths from the cells surrounding the carinal canals. These show a series of stages ranging from slight parenchymatous bulgings into the canal to its complete occlusion by a parenchymatous plug. Particles of soil also occur in the canal, and, where the occlusion is only partial, the quiescent cells have developed a well-marked cuticle. The ingrowths here recorded, although they offer an analogy to cavity parenchyma, differ from it in that they extend into a cavity which results from a protoxylem disruption preceding their formation.* A still closer parallel to the formation of cavity parenchyma is furnished by *Tradescantia virginica*, which has been described in detail by Gravis [**2**].

In this plant the xylem of certain of the bundles is defective, and its position is occupied by a lacuna, in which a few annular and spiral elements occur. With the approach of winter the aerial portion of the stem dies down, the internode situated at soil-level undergoing partial decomposition. Immediately below this level the lacunæ become occluded by thin-walled outgrowths derived from the small-celled parenchyma surrounding them. These outgrowths, which Gravis regards as strictly comparable with tyloses, penetrate and disorganize the protoxylem elements in precisely the same way as cavity parenchyma.

Whilst the formation of cavity parenchyma as distinct from tyloses is characteristic of existing ferns, it is worthy of note that true tyloses may be formed in response to traumatic stimulus. In the course of an investigation on the roots of the Marattiaceæ now in progress, a number of injured roots of *Marattia fraxinea* have been examined. Among the wound reactions shown by these, the closure of the metaxylem tracheids by typical tyloses is frequent, and illustrations of these are given in figs. 7 and 8. A classic instance of the development of tylose-like occlusions of the metaxylem elements in a fossil fern is provided by the petioles of *Ankyropteris corrugata*, in which they are extremely frequent, often completely blocking the whole of the tracheids. They also occur, though generally less abundantly, in the metaxylem of the rhizome and root. These structures were first observed and described by Williamson [**16, 17, 18**]. Dealing with them, he says [**18**, p. 320]:—"I think we shall not risk making any great mistake in concluding we have in them genuine examples of so-called thylosis. The structures so named vary in different examples, but it appears to me that the specimens now described approximate sufficiently closely to the general type of thylosis to be legitimately recognized as examples of it." Williamson's view has received considerable support from Weiss [**15**], but McNichol, on the other hand, is inclined to regard them as of fungal origin. If they are true tyloses, it is difficult to conceive of the function of an occlusion so widespread that it involves both rhizome and root as well as the petiole, unless it is assumed that it furnishes a means of blocking an effete portion of the conducting system. In view of its general occurrence in this species, it can hardly be regarded as pathological. A further difficulty, as McNichol points out, is the irregular nature of the distribution of the occluding growths, a peripheral tracheid being frequently quite free whilst a more centrally placed neighbour may be completely filled. If these occluding growths are derived from the conjunctive parenchyma of the stele, one would anticipate that the peripheral tracheids would show the phenomenon more markedly than those further from the margin. It is difficult, too, to conceive a method, apart from direct lateral penetration through contiguous pits from tracheid to tracheid, of invasion of the more centrally placed elements. Such lateral penetration may occur on a relatively small scale in the formation of cavity parenchyma,

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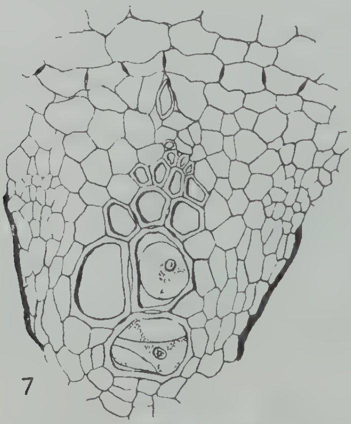
* I have recently noted a similar condition in a wounded internode of the aerial stem of *Equisetum limosum*.

Figs. 7–10.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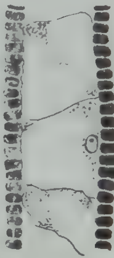
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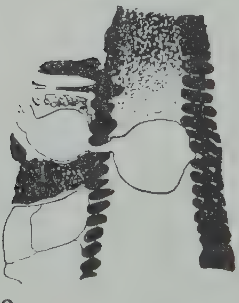
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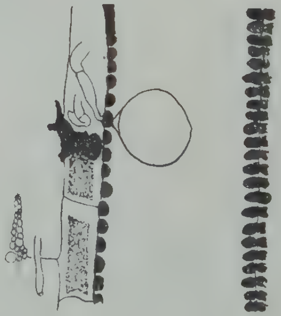
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Figs. 7–8. *Marattia fraxinea*—Transverse and longitudinal sections of a small part of an injured root, showing tyloses occluding the metaxylem elements (× 300).

Figs. 9 10. *Ankyropteris corrugata*—Fig. 9. Portion of two adjoining tracheids in longitudinal section, showing a tylose-like swelling passing from one tracheid to another [Nottingham Coll. 261.52]. Fig. 10. Longitudinal section, showing a vesicle-bearing fungal hypha passing from the conjunctive parenchyma into a tracheid [Nottingham Coll. B 24] (both × 400).

and McNichol figures a case in *Nephrolepis* in which three protoxylem elements are successively occluded by an outgrowth from one parent cell. The thickness of sections of fossil plants makes it peculiarly difficult to obtain evidence upon this point, and I have seen only one example in which connection is traceable between the occluding growths of contiguous tracheids. This is illustrated in fig. 9. Such lateral penetration does not in itself, however, serve to determine the nature of the ingrowths, since undoubted fungal hyphæ penetrate between the bars of the scalariform tracheids and may form vesicles. A case of this kind is shown in fig. 10, in which the section is unfortunately too thick to show the connection between vesicle and hypha adequately, although their orientation leaves little doubt as to their union.

Weiss suggests tentatively that their formation may be due to ingrowths from minute parenchymatous cells situated at the angles of the tracheids, but there does not seem to be any convincing evidence of the existence of such cells. On the other hand, a definite observation of a lignified tylosis such as that recorded by Weiss cannot be explained away, and lends support to their being regarded as true tyloses difficulties as to their method of formation notwithstanding.

It is obviously a difficult matter to obtain conclusive evidence for either opinion, but with a view to collecting further data, a systematic examination has been made of the slides of *A. corrugata* in the Scott and Williamson Collections in the Geological Department of the British Museum, and of the Cash and Hick Collections in the Manchester Museum, as well as of smaller series in the Nottingham and University College (London) Collections.

It soon became apparent that a record of the undoubted fungi occurring in association with *Ankyropteris* would be helpful, and accordingly a survey of the material from this standpoint was first made.

Four fungi which appear to be specifically distinct have been recognized, and three of these may be provisionally included in Seward's genus *Palæomyces* [**11**]. They consist of vesicle-bearing hyphæ similar to the forms described by Kidston and Lang [**5**] from the Rhynie cherts, and may be diagnosed briefly as follows :—

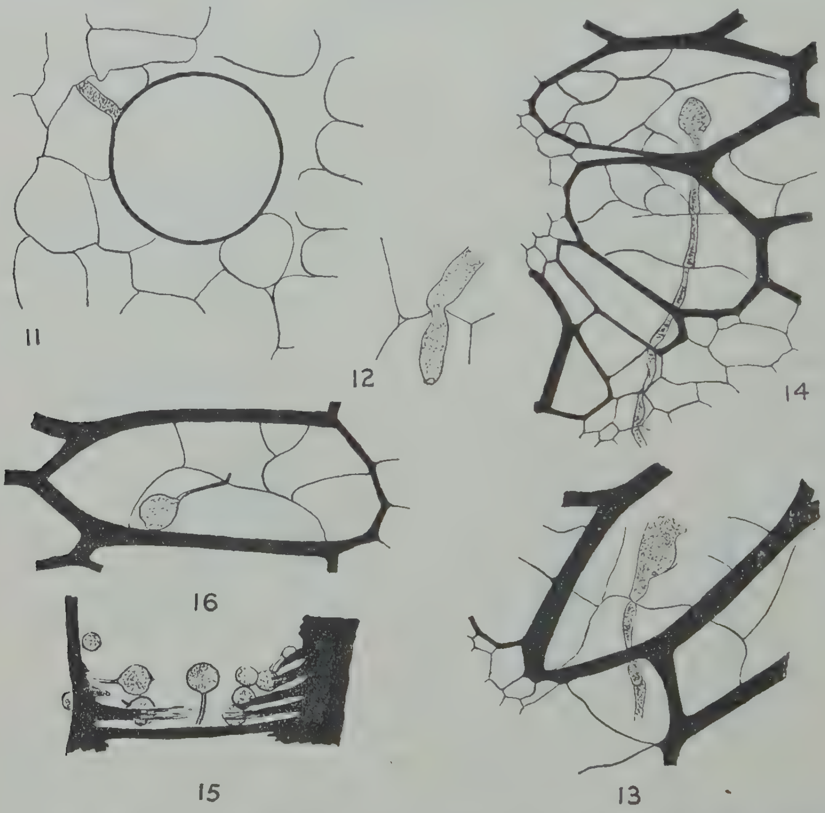
1. *Palæomyces α.*—Stout non-septate or sparingly septate hyphæ, 11–13 $\mu$ in diameter, bearing large terminal vesicles with firm relatively thick walls. The vesicles measured range in diameter from 130–160 $\mu$, with an average diameter, computed from twenty specimens, of 155 $\mu$. This fungus is common and generally distributed in all the plant-tissues in the matrix, and was presumably a constituent of the saphrophytic soil flora. A vesicle with hypha attached, growing in the inner cortex of *A. corrugata*, is shown in fig. 11 and a hypha passing from one cortical cell to another in fig. 12.

2. *Palæomyces β.*—Generally non-septate though occasionally frequently septate hyphæ, 8–10 $\mu$ in diameter and bearing thin-walled, mostly terminal

vesicles ranging in diameter from 25–70 $\mu$. This fungus occurs commonly in the parenchymatous tissues and tracheids of both *A. corrugata* and *Botryopteris tridentata*, and is shown in figs. 10, 13, and 14.

3. *Palæomyces* $\gamma$.—Delicate non-septate hyphæ, 3–5 $\mu$ in diameter, bearing small thin-walled vesicles 20–30 $\mu$ in diameter. This fungus occurs less commonly than the previous type, but in similar situations. There is some evidence that it is a saprophytic form, as it occurs abundantly in the stele and cortex of a much decayed oblique petiole section (Scott Collection, 2707).

Figs. 11–16.



Figs. 11–12. *Palæomyces* $\alpha$—Fig. 11. Typical thick-walled vesicle in the inner cortex of *Ankyropteris corrugata* [Manchester Coll. Q 71]. Fig. 12. Hypha piercing cell-wall [Nottingham Coll. 261.69] (both ×400).

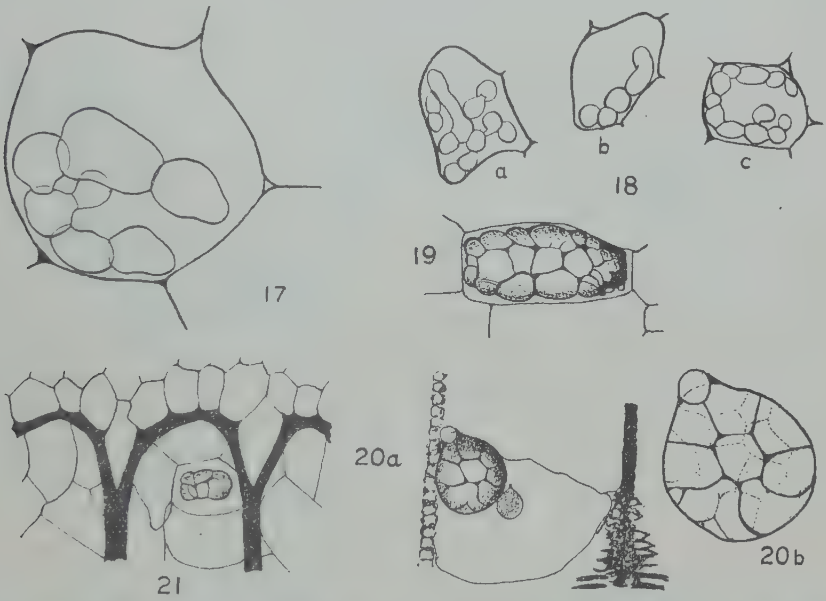
Figs. 13–14. *Palæomyces* $\beta$—Hyphæ bearing terminal vesicles and penetrating several cells. Fig. 13 [Nottingham Coll. 261.44]. Fig. 14 [Nottingham Coll. 261.47] (both ×400).

Figs. 15–16. *Palæomyces* $\gamma$—Hyphæ bearing terminal vesicles. Fig. 15 is from a partly decayed petiole [Scott Coll. 2707]. Fig. 16 shows a hypha penetrating from one tylose-like growth into another [Nottingham Coll. 261.75] (both ×400).

A portion of a tracheid from this petiole is shown in fig. 15, whilst other examples are shown in figs. 16 and 20 *a*.

4. *Halysiomyces ankyropteridis* *.—This fungus stands apart from the remainder, and its distribution suggests the possibility of its being mycorrhizal in nature. It consists of more or less ovoid cells, frequently drawn out into a neck-like constriction, where they unite with their fellows. They usually show a grouping and method of branching which is almost yeast-like (figs. 17–18). No hyphæ have been detected. They appear to pass into a resting stage in which the individual cells become thick-walled and closely aggregated, and polygonal as a result of mutual pressure. These cell-masses frequently take the shape of the cell in which they occur (fig. 19), but when not occupying the whole of the available space, they may assume a globular

FIGS. 17–21.



Figs. 17–21. *Halysiomyces ankyropteridis*—Fig. 17. Cell from the rhizome of *Ankyropteris corrugata*, showing typical method of growth of the fungus [Nottingham Coll. 261.69] (×750). Fig. 18 *a*, *b*, *c*. Other examples from the same rhizome (×400). Fig. 19. Assumed resting stage in which the cell-mass takes the shape of the containing cell [Manchester Coll. Q 71] (×400). Fig. 20 *a*. Resting stage, showing the globular form sometimes assumed. This particular example is lying within a tylose-like growth, and a vesicle of *Palæomyces* γ lies close to it [Nottingham Coll. 345.5] (×400). Fig. 20 *b*. The same, more highly magnified, the dotted lines indicating walls seen at lower foci. Fig. 21. Resting form composed of a small number of cells lying in a tylose-like growth [Nottingham Coll. 261.54] (×400).

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* Slides 2692 and 2693 in the Scott Collection show this fungus beautifully. They are referred to in Dr. Scott's Catalogue under 2693 as follows :—" Most of the cortical cells in this and other sections are full of granules like starch grains."

form (fig. 20). This fungus appears to be confined to the parenchymatous tissues of *Ankyropteris corrugata*, and is especially abundant in the cortical cells of the rhizome, being present in all the specimens examined. It is always intracellular, and frequently resembles a string of ovoid beads grouped round the periphery of the cell, though other more centrally situated cell-groups are visible at higher and lower foci. It occurs sparingly in the medullary parenchyma of the rhizome and in the inner cortex of the petiole and root. Typical examples are shown in figs. 17–20[*].

Apart from *Palæomyces* α, the relationship of these fungi to the tylose-like growths is one of considerable interest. With regard both to *Palæomyces* β and to *Palæomyces* γ, there is some evidence that infection of the tissues of *Ankyropteris corrugata* by their hyphæ post-dated the development of the tracheid-occluding growths. This fact is well shown for *Palæomyces* β in figs. 13 and 14, which illustrate cases in which it has been possible to trace a single hypha for a considerable length. In fig. 13 the hypha passes from one tracheid into another, and in the second tracheid penetrates the wall separating two adjacent occluding growths, whilst in fig. 14 the hypha passes out of the parenchyma separating the peripheral loop of small tracheids from the main tracheidal mass, through two tracheids, and into a third, piercing a whole series of occluding growths *en route*. The characteristic narrowing of the hypha at the points of cell-wall penetration is a feature which this palæozoic fungus shares with many existing species, and leaves no reasonable doubt that its entry into the tissues occurred subsequent to the formation of the growths which block the tracheids. Fig. 16 shows a similar condition in the case of *Palæomyces* γ. With regard to *Halysiomyces ankyropteridis* the case is somewhat different. It has been noted in several of the tylose-like ingrowths and always in what is assumed to be the resting condition. In these situations it sometimes consists of two or three cells only (fig. 21). If true hyphæ do not occur in this fungus, it seems probable that its presence in the tracheids is due to its being carried into them by the growths in which it occurs, so that its presence provides indirect support for the view which regards the latter as true tyloses.

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[*] HALYSIOMYCES, gen. nov.

Fungus endophyticus intracellularis pullulans, e cellulis ovoideis sæpe pyriformibus rarius allantoideis compositus, cellulis deinde intersese confertim aggregatis mutua pressione polygoniis pachydermaticis (quasi sporis perdurantibus), aut massulam subrotundatam aut ± irregularem efformantibus aut cellulam matricolem omnino explantibus.

An intracellular budding fungus, consisting of ovoid cells frequently drawn out into a short neck-like constriction at one end, where they are united to an adjacent cell; no hyphæ are developed, although occasionally more elongate sausage-shaped cells are produced; apparently possessing a resting stage in which the individual cells become compacted to form a cell-aggregate, become polygonal as a result of mutual pressure, and develop thicker walls; where the host-cell is completely filled the cell-aggregate assumes the shape of that cell, but where this is not the case a rounded or somewhat irregular group may be produced.

H. ANKYROPTERIDIS, n. sp.

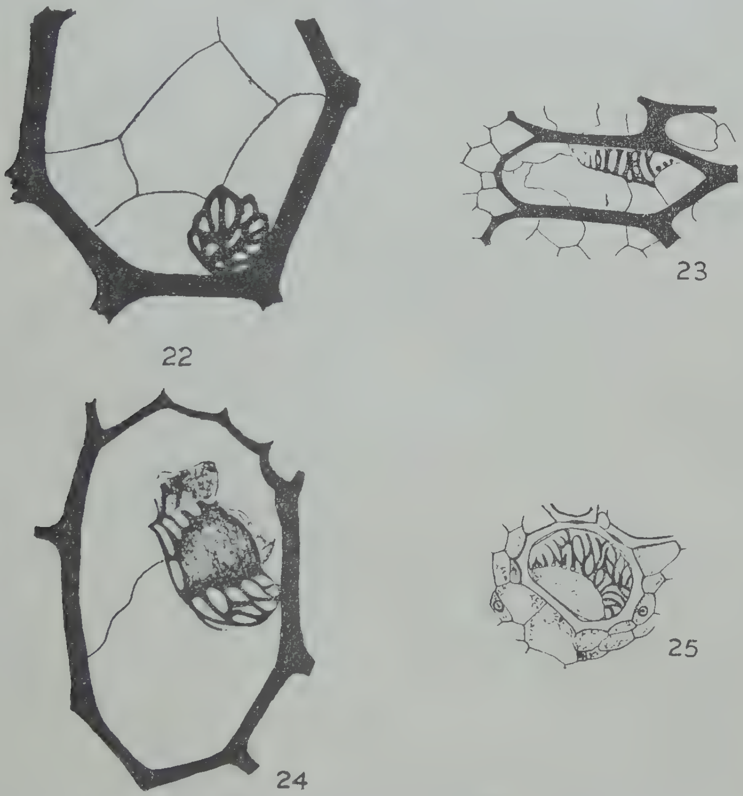
Cellulis aut ovoideis 35 μ × 33 μ–5 μ × 4·8 μ, aut insigniter elongatis 120 μ × 23 μ.

*Hab.* In fossilis filicis *Ankyropteris corrugatæ* rhizomate, in parenchymate corticali abundans, in parenchymate medullari minus frequens; etiam in parenchymate petioli et radicis corticis interni minus frequens.

A fungus with the above characters occurring abundantly in the cortical parenchyma of the rhizome of the fossil fern *Ankyropteris corrugata* and less commonly in the parenchyma of the medulla, and in that of the inner cortex of the petiole and root. Dimensions of individual ovoid cells ranging from 35 μ × 33 μ to 5 μ × 4·8 μ; of the exceptionally elongate cells the longest observed measured 120 μ × 23 μ.

Type-specimen. Slide 2692 [Scott Collection]. This fungus is also exceptionally well shown in Slide 2693 [Scott Collection] and in Slide Q 71 [Manchester University Collection].

Figs. 22–25.



Figs. 22–5. Fig. 22. *Ankyropteris corrugata*—Lignified "tylose" described by Weiss [Manchester Coll. R 448]. Fig. 23. Similar specimen in the Nottingham Coll. [261.74]. Fig. 24. Similar specimen in the Scott Coll. [2714]. Fig. 25. Lignified tylose in a metaxylem tracheid of the root of *Marattia fraxinea.*

This view receives further support from the discovery of other undoubted examples of lignified cells within the tracheids in addition to that described by Weiss. The additional examples are ten in number, six being in the Nottingham Collection, three in the Scott Collection, and one in the University College (London) Collection. The case described by Weiss (R 448, Hick Coll.) * is present in a petiole cut near its base before the characteristic peripheral loops have developed. It consists of a small, more or less discoid structure situated in the angle of one of the larger tracheids, and shows a reticulate type of thickening which at its free margin has a curious crenated appearance (fig. 22). The specimens in the Nottingham Collection are not so heavily thickened, and in most of them the lignification is spiral in type, with occasional cross-connections suggesting a transition to the reticulate condition (fig. 23): one, however, is reticulate. Of those in the Scott Collection one (Slide 2714) occurs in a petiole which is still united by its cortex to the parent rhizome and, like that in the Manchester slide, is reticulate in type (fig. 24). The most interesting specimen in this collection, however, is one occurring in a longitudinal section of a stem (Slide 2692) in which a vertical row of lignified tyloses is present. The University College specimen (Slide K 610) is also a longitudinal section of a stem and shows two examples of tracheid occlusion by lignified tyloses. In the tyloses occurring in the roots of *Marattia fraxinea*, to which reference has been made earlier, lignification is not uncommon (fig. 25), and it is interesting to note that both spiral and reticulate types of thickening occur as well as transitional forms, so that in this respect they are closely comparable with those occurring in *Ankyropteris corrugata*. A crenation of the free margin similar to that shown by Weiss's specimen is not infrequent in *Marattia*, but by careful focussing it is generally possible in the recent examples to distinguish the delicate cellulose wall of the parent cell. It seems probable that, in the case of the fossil specimen, the preservation was not sufficiently perfect to enable us to distinguish this feature. Since the occurrence of lignified fungal hyphæ is unknown, it is evident that the balance of the available evidence supports the view that the occluding growths in the tracheids of *Ankyropteris corrugata* are true tyloses, although some of the difficulties presented by their distribution remain unsolved.

## *Summary.*

1. Cavity parenchyma, though generally confined to the petiolar protoxylem areas in the Filicales, frequently occurs in similar areas in the rhizomes of *Pteridium aquilinum*.

2. In this species it occurs chiefly in the outer ring of meristeles, and is only found occasionally in the inner system.

3. It also occurs sometimes in the rhizome of *Matonia pectinata*.

4. An analogous type of parenchymatous ingrowth may be formed in the internodal carinal canals of the rhizome of *Equisetum arvense* as a result of wounding.

5. True tyloses, resulting in the occlusion of the metaxylem, occur in wounded roots of *Marattia fraxinea*. These may become lignified.

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* The catalogue number of this slide is erroneously given as R 447 by Weiss [**15**].

6. The evidence as to the nature of the growths occluding the metaxylem elements in the fossil fern *Ankyropteris corrugata* is reviewed, and is held to support the view that they are true tyloses.

I should like to express my thanks to the Keeper of the Geological Department, British Museum, for permission to study the slides in the Williamson and Scott Collections; to Mr. W. N. Edwards, for many kindnesses whilst working at the British Museum; and to Professor F. E. Weiss and Professor F. W. Oliver, for the loan of slides of which they have charge. To Mr. J. Ramsbottom and Mr. F. T. Brooks I am indebted for information with regard to the behaviour of fungal hyphæ and also to the former for the Latin diagnosis of *Halysiomyces*.

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# Some Critical Species of *Marrubium* and *Ballota*, and a Note on *Colchicum montanum* Linn.

By C. C. LACAITA, F.L.S.

(PLATES 2 & 3 and 3 Text-figures.)

[Read 8th January, 1925.]

IN the 'Species Plantarum' of 1753, and again in the second edition without material alteration, Linnæus does no more than repeat, in most cases *totidem verbis*, the diagnoses of the species of *Marrubium* that he had already published in the 'Hortus Cliffortianus' of 1737. Several of the synonyms and part of the observations are omitted in the latter work, presumably for the sake of brevity. One or two fresh synonyms are introduced, but the only material changes are the subdivision of *M. peregrinum* in (α) and (β), and of Hort. Cliff. no. 8 into two species, *Pseudo-Dictamnus* and *acetabulosum*. It follows that in this genus, with one exception mentioned hereafter, the specimens of the Clifford herbarium carry more weight than those of Herb. Linn. in elucidating the author's meaning. They are not unfrequently in conflict. In this case, as in sundry others, Linnæus seems to have forgotten in 1753 his earlier knowledge of plants described in Hort. Cliff., of which he no longer possessed the specimens.

In Sp. Pl. he enumerates four species "*calycibus* 5-*dentatis*" and five "*calycibus* 10-*dentatis*." Of the latter all but *Marrubium vulgare* have since been transferred to the genus *Ballota*, and none of them will come up for remark except *M. hispanicum*. Of those with five calyx-teeth, the first, *M. Alysson*, is represented in both herbaria and raises no problems. The remaining three have long caused perplexity, due in varying degree to lack of specimens, to similarity of forms, to slips of the pen or of the printer, and to disagreement between text and specimens.

## I.

### MARRUBIUM CANDIDISSIMUM.

This name has always been applied in modern times—though wrongly, as Dr. Degen has pointed out in a recent paper "Ueber *Marrubium candidissimum* L." in Bot. Közlem. xx. (1922)—to a well-known species found on both sides of the Adriatic, with white, almost silvery foliage, whorls of many flowers, and bracts as long as or longer than the tube of the calyx, whose teeth are longer and more divergent in fruit than in any other species here spoken of. The earliest distinctive name for this plant is certainly, as Dr. Degen declares, *M. incanum* Desr. in Dict. Encyc. iii. p. 716 (1789).

The identity of Desrousseaux's species is conclusively established by his description, his reference to Hort. Elth. fig 215, and the specimen labelled *incanum* in Herb. Lamarck, which I have inspected *. It will appear directly that Linnæus knew, or ought to have known, this plant, but he included it in his composite *peregrinum α*, and did not refer it to his *candidissimum*.

What then did he mean by *candidissimum*? All that he says in Sp. Pl. is to quote his own diagnosis of no. 4 in Hort. Cliff., *M. foliis subovatis lanatis, superne emarginato-crenatis, denticulis calycinis subulatis* †, and to refer to *M. album candidissimum et villosum* Tourn. Cor. p. 12 as a synonym. Unfortunately Tournefort's plant is untraceable, so the only help this synonym gives us is to establish that *candidissimum* is not a European but an Oriental species, like all the others comprised in the 1356 enumerated in the "Corollarium in quo plantæ in Orientalibus Regionibus observatæ recensentur."

In Tournefort's herbarium at Paris the name only occurs on the label of specimen no. 1290, which reads: "*Marrubium album græcum foliis ad basin acutis*; *Marrubium album candidissimum et villosum* Coroll. Inst." The plant on the sheet, and a similar one on a second sheet which bears no label, is only a form of *M. vulgare*, with characteristically uncinate calyx-teeth, ten in number. It is less tomentose, and with less rugose leaves than usual in *vulgare*; the leaves being cuneate rather than ovate at the base. Similar specimens occur in herbaria from very different parts of the area of the species; for instance, Tossia in Asia Minor, Palermo, Morocco, the Swiss Valais, Södermanland in Sweden, and Hoboken near New York. Now either, as seems probable, the words *M. album candidissimum et villosum* have no business on the label of this specimen, or else, if this is really what Tournefort meant by that name, it cannot possibly throw any light on a species which Linnæus has placed among those with only five calyx-teeth, those teeth being not uncinate but subulate.

We are therefore thrown back on the diagnosis, on the specimens, and on a supplementary reference in Syst. ed. xii. p. 396 (1767) to a figure in the 'Hortus Elthamensis.' The diagnosis first appears in Hort. Cliff., and is merely repeated in Sp. Pl. with the slight modification of *dentibus subulatis* instead of *setaceis*, which for the moment we may assume to have been a slip of the author's pen or of his scribe. If, therefore, we should find that the specimens in Herb. Hort. Cliff. differ from the corresponding ones in Herb. Linn., it is obviously on the plant from Clifford's garden, and not on specimens acquired at a much later date, that Linnæus based his diagnosis.

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* There is another specimen of the same in Herb. Lamarck, labelled *candidissimum*, although Desrousseaux catalogues *M. candidissimum* Linn. as unknown to him. It follows that Lamarck's herbarium is not always to be relied on for identification of names in the Dict. Encyc.

† *Setaceis* in Hort. Cliff. See p. 159 as to this alteration.

Now, what do we find in Herb. Hort. Cliff.? Two specimens, of which Pls. **2** & **3** show photographic reproductions, labelled respectively *Marrubium folio rotundo candidissimo* and *Marrubium folio candidissimo orbiculari*. These have been subsequently labelled by some post-Linnean hand *candidissimum* and *candidissimum* (cancelled by a stroke of the pen) *peregrinum*, the last a bad shot to which we need pay no attention. The original phrase-names are those of *Marrubium* no. 2 and *Marrubium* no. 8 in Boerhaave's Hort. Lugd. pp. 136, 137 (1720), to both of which Boerhaave has set the query, "An *Marrubium album candidissimum et villosum* T. Cor.?" Both of the phrases are quoted in Hort. Cliff., though omitted in Sp. Pl., as synonyms of *Marrubium* no 4. It looks as if these plants grown for Clifford had been received from the Leyden gardens, the source from which Dillenius tells us that they came to Eltham, and that Linnæus, when compiling his account of Hort. Cliff., had copied the Tournefort synonym from Boerhaave without inquiry and omitted the interrogation. We shall see directly that there is reason for holding that synonymy to be wrong.

Now examine the specimens themselves; after very careful inspection I think they may both be determined as garden-grown examples of *Marrubium globosum* Montbr. & Auch., a species from Asia Minor described in Bentham's "Labiatæ orientales herbarii Montbretiani," Ann. Sci. Nat. sér. 2, vi. p. 53 (1836), and very nearly allied to *M. astracanicum* Jacq. Linnæus's diagnosis, as far as it goes, agrees much better with these specimens and with others of *globosum* * than with *M. incanum*, the leaves of which could not rightly be called *suborata apice emarginato-crenata*. To clear the ground we may point out that *M. album candidissimum et villosum* cannot be *incanum* Desr., because Herb. Tourn. no. 1285, which obviously is *incanum*, bears the label *M. album latifolium peregrinum* C. B. P., an interpretation of Bauhin's name to which Linnæus also shows some partiality. For a guess as to the meaning of Tournefort's *album candidissimum et villosum* see below under *M. circinnatum*.

So far we may say that *Marrubium* no. 4 of Hort. Cliff. and the two specimens representing it are *M. globosum*. Now, if at a later date Linnæus, without materially altering his diagnosis, laid in his herbarium a totally different plant for his *candidissimum*, that would merely amount to a false determination of an individual specimen, not to a complete change in the connotation of a specific name. This is just what he has done, for in Herb. Linn. on the sheet now no. 3 there lies an unmistakable *M. incanum*, sine loco, alongside of a smaller piece of a very dissimilar plant, *M. supinum* Linn.* There is only one label for both, written by Linnæus himself, which at first read *peregrinum*, but this word was subsequently cancelled by a stroke of the pen, and *candidissimum* substituted, also in Linnæus's hand. Such a muddled sheet cannot possibly overrule the diagnosis of *candidissimum* with which both pieces disagree. Moreover, there is pinned (when? by whom?) to that sheet another, no. 4, which is one of those originally belonging to Hort. Cliff., but later cut down to the size of the sheets in Herb. Linn. The specimen is so arranged as to appear to grow out of the well-known flowerpot design of Herb. Hort. Cliff. It is very perplexing at first sight, for though it looks like the other two Hort. Cliff. specimens already mentioned, the basal leaves are something totally different. There is no writing on the face of the sheet except the one word *Marrubium* at the top, but on the back we read "*Sideritis cretica tomentosa candidissima, flore luteo* T. cor. 12. *Stachys minor italica* C. B. P. 236 et *Pilosella syriaca* C. B. P. 262." On more careful inspection it becomes evident that the stem and upper part are not attached to the root-leaves, and that while the upper part is in fact a *Marrubium*, the root-leaves are indeed those of *Sideritis syriaca* Linn.!! What are we to say then? That *Marrubium candidissimum* is *M. incanum* Desr. on the sole evidence of sheet no. 3? Surely not; it is too clearly an Oriental species, in spite of the impossibility of ascertaining the real meaning of the Tournefort synonym.

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* The examples of *M. globosum* on which I have relied for comparison are: (1) Aucher-Eloy, no. 1787, from Ak-Dagh in the Taurus; (2) C. Pinard, anno 1843, from Caria; (3) Boissier, from M. Cadmus above Gheyra in Caria; (4) Bourgeau, from Ak-Dagh in Lycia, distributed under the wrong name of *micranthum*; (5) Pichler, from Bei-Dagh in Lycia; (6) Bornmüller, pl. exs. Anatoliæ or anno 1889, no. 607, from Amasia; (7) Siehe, anno 1895, no. 215, from Cilicia, wrongly named *M. heterodon* in Herb. Kew.

There is yet more evidence: in Syst. xii. p. 396 (1767) Linnæus quotes for *M. peregrinum* a figure in Hort. Elth. (1732) as 219, tab. 175, f. 214, and for *M. candidissimum* 218, tab. 174, f. 214. Here there are two misprints, repeated in later editions: tab. 175 does not show a *Marrubium* but *Horminum*. In both cases tab. 174 is meant; but then fig. 214 is quoted twice and fig. 215 is omitted. Fortunately I have been able, with the assistance of Dr. Daydon Jackson, to find the clue to what Linnæus intended to say. The plate in question, tab. 174, contains two figures, 214 on the left, 215 on the right. In his own copy of Hort. Elth. Linnæus wrote *candidissimum* below the left-hand fig. 214 and *peregrinum* below the right-hand fig. 215. That copy can no longer be traced; it was once in Smith's possession, but he sold it to Dr. Woodward and retained his own copy, now in the library of the Linnean Society, "*prout optimum*," as he wrote in the margin of an old MS. catalogue now belonging to the Society. Very wisely, before parting with Linnæus's copy, he transcribed the above identification at the foot of the plate in the copy now with the Society †. This MS. note of Linnæus proves conclusively that at the date when it was written he regarded *incanum* as referable to his *peregrinum*, for fig. 215 is precisely Desrousseaux's species, whereas fig. 214 is obviously not *incanum*, but to my eyes appears to be *globosum*, or at any rate the Hort. Cliff. plant which I have determined as such. The conclusion is quite clear; the name *candidissimum* Linn. cannot be used for the Adriatic *incanum* Desr., but if the identification of the Hort. Cliff. specimens with *globosum* be accepted, it would take the place of that name.

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* It is surprising to find this particular confusion with *supinum* among Linnean specimens, though it is one often made by earlier authors, as by Dillenius Hort. Elth. in the synonymy for his fig. 215.

† Visiani, Fl. Dalm. ii. p. 217, though unacquainted with this MS. note of identification, points out that fig. 215 is precisely the *candidissimum* of the 'Flora Dalmatica,' i. e. *incanum* Desr., and that fig. 214, quoted by Linnæus for *candidissimum*, does not represent either *incanum* or *peregrinum*. We may ignore the absurd mixture of synonyms which Dillenius himself quotes for fig. 215.

There are still some minutiæ to notice. As already mentioned, the phrase *denticulis setaceis* of Hort. Cliff. is altered to *denticulis subulatis* in Sp. Pl. for *M. candidissimum*, but on the other hand *M. peregrinum* becomes *denticulis setaceis*, whereas in Hort. Cliff. it was *denticulis subulatis*. As in Sp. Pl. Linnæus only quoted the diagnoses from Hort. Cliff., it is not improbable that the exchange of the two words subulate and setaceous was unintentional, and is due to a slip of some copyist. That no change was intended is, I think, supported by the observation in Hort. Cliff. under no. 4, "*ad antecedentem proxime accedit, sed folia crassiora et dentes setacei rigidiusculi.*" So here we have the *dentes setacei* twice repeated. The descriptions of later authors, *e.g.* Bentham and Boissier, assign to *peregrinum* calyx-teeth with a wider base (i.e. *subulati* not *setacei*) than in other nearly allied species. This is in agreement with Hort. Cliff., and an additional reason for thinking that the alteration in Sp. Pl. was accidental.

The habitat for *candidissimum* is given in Hort. Cliff. as "*Creta, ut fertur*," in Sp. Pl. as "Creta?" A very usual guess in those days as to the source of plants of unknown origin. As a matter of fact, neither *incanum* nor *globosum* is found in the island, though possibly *peregrinum* in the form of *creticum* Mill. grows there.

## II.

## MARRUBIUM PEREGRINUM.

*Marrubium peregrinum* Linn. is a composite species in which Linnæus distinguishes an ($\alpha$) synonymised with *M. alterum pannonicum* Clus. and *M. album latifolium peregrinum* C. B. P., and a ($\beta$) identical with *M. album angustifolium peregrinum* C. B. P. and *M. creticum* Dalech., which afterwards became *M. creticum* Mill.

It will be convenient to take ($\beta$) first, as its identity is so well known. It is *M. peregrinum* Jacq. Fl. Austr. tab. 160, a species which ranges from Prussian Saxony across central Europe to Greece, and possibly to Crete. It grows very plentifully near Vienna, whence it has been distributed in Fl. Exsicc. Austr. Hung. no. 171. This is the plant usually understood by continental botanists under the name *peregrinum*, though Reichenbach, Ic. Crit. iv. p. 75 (with an admirable figure, no. 461, agreeing with Jacquin's plate), and Celakovsky, Prodr. Fl. Böhm. p. 841, prefer to use the name *creticum* Mill. It first appears in Pena & Lobel's Stirp. Adv. Nov. p. 222 (1576), with a Plantinus woodcut, as *Marrubium creticum angustiore folio*, *odore gratiore*, quoted by C. Bauhin as synonymous with his *M. album angustifolium peregrinum*. The same woodcut reappears in Dalechamp. Hist. Pl. p. 692, as *M. creticum* Penæ. The claim of this plant to grow in Crete is doubtful*. Smith in Fl. Gr. Prodr. certainly records it for the island as *M. creticum* W., *M. peregrinum* β Linn. On the other hand it has never been found there by any later collector than Sibthorp. The specimen in Sibthorp's herbarium—precisely the species of which we are speaking—is *sine loco*, and whatever evidence Smith may have possessed that it really came from Crete and not from the mainland of Greece, is now lost. Smith often made mistakes as to the origin of Sibthorp's specimens. This one agrees perfectly with Heldreich's Herb. Græc. Norm. no. 60 from Parnassus. Both are remarkable for their very small bracteoles, shorter than in the Austrian type. The Hort. Cliff. specimen of *M. album angustifolium peregrinum* belongs to this *peregrinum β*, so does the *M. creticum* in herb. Lamarck, but those of herb. Tournefort which should represent it do not. Herb. Linn. also contains a surprise or two under the name *peregrinum*, which will be mentioned below. Meanwhile there seems to be no sufficient reason for disturbing the current use of "*peregrinum* Linn." for this species, although it is a β. In this case to attempt to restrict the employment of the name to α would lead to irreconcileable differences of opinion.

It is on turning to *peregrinum* (α) that we encounter serious difficulties. Is this just the plant of Clusius, *M. alterum pannonicum*, or is it *M. incanum*, or a muddle of both? Linnæus has certainly mixed up these under (α) and possibly *M. paniculatum* Desr. and *M. præcox* Janka as well. This is the justification for preferring (β) as entitled to the specific name in this case. Of the two synonyms quoted, that of Clusius is the really important one. *M. album latifolium peregrinum* C. B. P. is not a little confused, as has been pointed out by Kerner †, and may be seen by reference to the conflicting older names quoted for it by Bauhin himself, Pin. p. 230. Morison's figure, Hist. iii. s. 11, tab. 9, fig. 8, cited by Linnæus in support of it, evidently represents the same plant as that of Clusius ‡, who in Rar. Stirp. Pann.

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* Of course no weight attaches to Miller's geography; the countries of origin in the Gardener's Dictionary are frequently unreliable. I have previously had occasion to point this out in Nuov. Giorn. Bot. It. xxv. p. 39 in respect of *Dianthus ferrugineus*. Another obvious case is *Pulmonaria saccharata*; but in the genus *Marrubium* Miller excels himself. For his no. 3, *creticum*, he assigns Spain and Portugal; no. 5, Spanish *M. supinum*, he banishes to the islands of the Archipelago; no. 6, the certainly Oriental *candidissimum* etc. of Hort. Cliff., flies west to Spain, an impossible habitat even if *M. incanum* were intended.

† Kerner's important discussion of *M. peregrinum* and *M. remotum* in Oestr. Bot. Zeit. xxix. (1874) pp. 339–342, is referred to.

‡ In the separate detail the calyx seems to show more than five teeth, but this is probably bad drawing, as it is shown with five on the plant, and in the text, p. 377, Morison says "calycibus quinquefariam in margine divisis."

(1583) had described and figured, as *Marrubium alterum pannonicum*, a species which he declares to be very common in Austria and Pannonia. "Adeo vulgare est in toto Viennensi agro, ut vinetorum agrorumque margines, siccique et graminei campi eo abundent." It would seem to be on this figure of Clusius that C. Bauhin based his *M. album latifolium peregrinum*, and it is regarded by Jacquin as being the very plant depicted in his tab. 160. Now it is certain that the plant of Clusius's woodcut is not *incanum*, though it differs somewhat in leaf-outline from Jacquin's. Was it nothing but a broader form of the common Viennese plant? ; in which case the difference between *latifolium* and *angustifolium* would shrink to one too slight for Linnaeus to have subdivided his species on that ground alone. Quite another view is taken by such eminent botanists as the elder Reichenbach, Koch, Bentham, and Boissier, who all refer Clusius's name and figure to a different species, usually known as *M. remotum* Kit. (in Schult. Oesterr. Flora, ed. 2, ii. p. 161, 1814), but of which *M. paniculatum* Desr. (in Dict. Encyc. iii. p. 716, 1789) is the earliest name.

Kerner has completely demolished this theory. Although *M. paniculatum* grows in Austria as well as in Hungary, it is exceedingly rare near Vienna, where it occurs only occasionally in the company of *M. peregrinum* and *M. vulgare*, between which it has been considered by most Austrian botanists to be a hybrid. It cannot be supposed that Clusius was speaking of so rare a plant when he said, "*vulgare est in toto Viennensi agro.*" It is the figure—the figure only and no words of Clusius—that led Reichenbach, Koch, and the rest to identify *M. alterum pannonicum*, and consequently *M. peregrinum* (α) with *M. paniculatum*. The figure indeed has more likeness, owing to the broader leaves, with rather sharper serratures and the longer bracts, to Reichenbach's plate of *paniculatum* in Ic. Crit. iii. fig. 473 than that of *creticum*, ibid. fig. 461. But Clusius has distinctly shown the calyces with five teeth, as they constantly are in *creticum*, whereas in *paniculatum* they are irregular in number, between 5 and 10. The conclusion is that Clusius meant the very same plant as Jacquin, in spite of the broader leaves of the figure. As Kerner points out, the earlier leaves of *peregrinum* are always broader than the later, so that the appearance of a specimen depends much on the stage at which it is gathered, and in those from hotter or drier countries the broad leaves fall away sooner than in milder climates. We must therefore reject the synonymy given by Koch in all editions of the Synopsis before the last. "*M. peregrinum* L. occurrit (a) *latifolium* = *M. peregrinum* W. = *M. paniculatum* Desr. = *M. remotum* Kit. ; (b) *angustifolium* = *M. peregrinum* Jacq. = *M. creticum* Mill." In the last edition Brand alters this by confining the name *peregrinum* to (β) and transferring (α) to a separate hybrid species.

But merely to unite (α) and (β) as insignificant forms of one species, as in

Schedæ ad Fl. Exsicc. Austr. Hung. no. 171, is too ingenuous. The case is not so simple as that. When the Linnean specimens are examined they show among other things that Linnæus included under *peregrinum* (α) not only the plant of Clusius but also *incanum*, being apparently unconscious of the contradiction. Thus in Herb. Hort. Cliff. the specimen of *album angustifolium peregrinum* is precisely Jacquin's plant, but *album latifolium peregrinum* is represented by an example of *incanum*. In Linnæus's own herbarium we find for *peregrinum* (without distinction of (α) and (β)) the sheet no 3 already mentioned, containing both *incanum* and *supinum* but no true *peregrinum* (*creticum*), on which the label has been altered from *peregrinum* to *candidissimum*. This sheet then, before the alteration of the label, so far agreed with the Hort. Cliff. specimen and with Linnæus's note to Hort. Elth. fig. 215 as to indicate *incanum* as being *peregrinum* (α). Of course one would like to say on the strength of these specimens and of the note, "Koch as well as Kerner are all wrong; *peregrinum* (α) is neither *remotum* nor Jacquin's *peregrinum* but *incanum*, which would otherwise be entirely omitted by Linnæus, an untenable supposition, since it exists in both herbaria and, as already explained, cannot be *candidissimum*." But then we should contradict the only reliable synonym, that of Clusius, and also that of Morison and to a great extent that of Bauhin also. The only possible conclusion is to drop the use of the Linnean name for the plants confused under (α) and restrict it to the well-defined (β) with narrower or wider leaves. We may safely do this in spite of the hitherto unnoticed incompatibility of yet another specimen. As already mentioned, the Hort. Cliff. example of (β) is Jacquin's species, but the corresponding one in Herb. Linn., now bearing the number 2, is something else. It is named by Linnæus "*peregrinum* (β)" with "*M. album angustifolium* C. B." written on the back, and is marked ε, showing that he had received it from Gerber, who travelled in south-eastern Russia. It is also labelled in another hand—perhaps Gerber's own—"*Marrubium album angustifolium* ad fluv. Axey." This is an old spelling of Ak-sai, the name of two rivers Yesaulovskoi Aksai and Kurmoyarski Aksai, which rise in the western hills of Astrachan and flow westward into the Don. The usual maps and gazetteers will show the town Aksai even if the rivers are not marked. There are in the possession of the Linnean Society two MS. lists of plants collected by Gerber. No. 1, Flora Wolgensis, under no. 1064 names *M. album angustifolium peregrinum* as growing "in desertis Donnensibus inter Glasunowski et Saratowa"; no. 2, Flora Tanaensis, which is in the handwriting of Linnæus himself, contains no 1522 "*M. album angustifolium*, ad fl. Axey." The specimen itself is a good example of *M. præcox* Janka, in Oestr. Bot. Zeit. xxv. (1875) p. 62, a species which extends from Transylvania eastward and seems to be plentiful in southern Russia, though often unrecognised. I have myself an example collected by Zohrab at Berdiansk on the sea of Azov in 1869, which is identical with that of Linnæus*. In habit *M. præcox* resembles *M. paniculatum* more closely than *M. creticum*, and has been mixed up with it by Boissier in Fl. Or. iv. p. 792. They are often confused and wrongly labelled in herbaria. Here are Janka's distinctions: "*M. peregrinum*" (*creticum*); "calycis tubus obconico-campanulatus; dentes semper 5 triangul-acuti, crassi, recti; basi sinu acuto confluentes. *M. præcox*; calycis tubus cylindricus; dentes semper 5 subulato-setacei tenues recti; basi interstitio sejuncti." I may add that in *præcox* the bracts are a good deal longer than in *creticum*, though not so long as in *incanum*, and the serratures reach nearly to the base of the leaf. *M. paniculatum* is, of course, distinguished by its larger number of calyx-teeth. The superficial resemblance of the Linnean specimen of *præcox* to *creticum* is quite close enough to account for its having been unsuspiciously passed as *peregrinum*; it need not disturb our acceptance of *creticum*, Jacquin's plant, as being the true and only heir to the Linnean title *peregrinum*.

One word as to the *habitat* assigned by Linnæus for *M. peregrinum*. In Hort. Cliff. he says, "circa Messanam Siciliæ, in Creta et in agro Viennensi"; in Sp. Pl. "in Siciliæ, Cretæ, Austriæ siccis" and in ed. 2 he adds "in Libano" for *peregrinum* (*β*). Crete and Vienna have already been discussed; in the absence of a specimen it is impossible to say what the reference to Lebanon means; the only species mentioned in Fl. Or. for those mountains being *M. cuneatum* and *M. libanoticum*, neither of which resemble *peregrinum*.

The Italian floras, *e.g.* Fl. Anal. d'Italia, iii. p. 20, are not aware of the presence of either *incanum* (their *candidissimum*) or *peregrinum* in Sicily. I was therefore surprised to find in Herb. Gay at Kew a specimen of *incanum* sent from that island by Jan as *M. candidissimum* Linn. and included in his 'Elenchus' of 1827, p. 9, as well as another in Herb. Mus. Brit. received from Gandoger with the label "*Marrubium candidissimum* in Sicilia prope Caltanissetta legit Reimbole, Septr. 1872." It therefore seems probable that the *M. supinum* quoted by Ucria, Hort. Pan. p. 248, for Sciacca on the south coast of the island is *incanum*. The presence of *peregrinum* in Algeria is uncertain; *cf.* Battandier, Fl. Alg. p. 695.

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* For *M. præcox* I rely also on (1) J. Barth, anno 1895, from Márog-Hudoz in Transylvania; (2) Sintenis, anno 1873 no. 275, from Babadagh in the Dobrudscha (as *M. remotum*); (3) Nordmann in herb. Bentham, from Odessa (as *M. peregrinum*); (4) Callier, It. taur. secund. 1896 no. 180, from Burunduk in the Crimea; (5) Herb. Flor. Rossiæ no. 835, "in steppis prope urbem Taganrog." This is near Gerber's locality. The label includes an obs. by D. Litwinow: "*M peregrinum* L. in Caucaso videtur vulgatissimum septentrionem versus, in steppo Rossiæ meridionalis valde rarescit."

## III.

### MARRUBIUM PANICULATUM.

The discussion of *M. peregrinum* has called our attention to *M. paniculatum* Desr., in Dict. Encyc. iii. p. 716 (1789). This species is more usually known as *M. remotum* Kit. in consequence of a doubt as to the identity of *paniculatum* expressed by Bentham, Lab. p. 590, under *M. pannonicum*, for which I see no sufficient reason, although the synonyms quoted are rather mixed and the chief characteristic—the number of calyx-teeth—is not mentioned. Herb. Lamarck contains a specimen agreeing with *remotum*, originally labelled *paniculatum* although the label has been subsequently altered to *peregrinum*, which it is not. *Peregrinum* = *creticum* appears both in Dict. Encyc. and in Herb. Lamarck under the latter name. Herb. Tournefort contains two sheets, 1287 and 1288, referable to *paniculatum*, although labelled *M. album angustifolium peregrinum*, of which there is no true example in that herbarium. Reichenbach adopted Desrousseaux's name in Ic. Crit., although he thought it "*nomen ineptum*," but for that reason he altered it in Fl. Germ. Exc. p. 325 (1830) to *M. pannonicum*, regardless of the existence of the earlier *M. remotum* Kit. of 1814.

Most Austrian botanists have adopted the view of Reichardt, in the Vienna zool.-bot. Verhandl. xi. p. 342 (1864), that *paniculatum* is nothing more than a bastard between *vulgare* and *peregrinum*. This suggestion must have been put forward at a much earlier date, though ignored by Kitaibel, Koch, and the Reichenbachs, because it is criticised by Bentham, Lab. p. 591, on the ground that "natural hybrids appear scarcely possible in a genus where, like *Marrubium*, the stamina and style are enclosed in the tube of the corolla." Such an objection can hardly be sustained. There lies before me a very evident hybrid between *supinum* and *vulgare* collected by Pau near Segorbe in Spain. There is, however, another side to the question. Kerner, *loc. cit.*, points out that although in Germany, where it is found at Erdeborn near Halle, and in Austria, this is a rare plant only seen where its presumed parents grow; it is widespread in Hungary, very plentiful where it occurs, often present where there is no *vulgare*, outnumbering *peregrinum* where they grow together, here and there covering whole stretches of country and spreading itself successfully by seed.

All that is very unlike the behaviour of an ordinary bastard. I must confess that in the specimens I have seen I can discover little or no evidence of hybridity with *vulgare*. The calyx-teeth, although more numerous than in *peregrinum*, have no resemblance to those of *vulgare*, nor have the leaves. If it were not for the opinion of those who know the plant in its natural surroundings, I should refuse to admit its hybridity on herbarium evidence alone. Some further details may be found in a paper by Borbas, "Zur Flora von Mittel-Ungarn," in the same vol. xxiv. of Oestr. Bot. Zeit. p. 343. These do not seem to be quite in accord with Kerner's assertions. Kerner suggests, however, that the plant is an instance of the establishment of an independent species from originally hybrid individuals, and adduces it in his paper "Können aus Bastarten Arten werden?" in Oestr. Bot. Zeit. xxi. (1871). Is it not possible that all the individuals found in the western part of the area, where *paniculatum* fails to spread itself, and also some of those in Hungary, may be hybrids in the ordinary sense, while more favourable conditions in other districts have led to its establishment independently of the parents? A final explanation must rest with Hungarian botanists who can follow up the different forms in the field. It must not be forgotten that at the date of Kerner's paper Janka's *M. præcox* had not yet been distinguished. Though referred to without being named in Borbas's paper, it was not published till the following year, 1875.

## IV.

### MARRUBIUM SUPINUM.

This Spanish species, which extends to Algeria, affords another instance of the greater reliability of specimens in Herb. Hort. Cliff. than of those in Herb Linn. in this genus. *M. supinum* of Sp. Pl. is identical with no. 6 in Hort. Cliff., defined as *M. denticulis calycinis rectis villosis*, with references to *M. album sericeo parvo et rotundo folio* Barr. Ic. 685 and *M. hispanicum majus* Barr. Ic. 686, as well as to *M. hispanicum supinum foliis sericeis argenteis* Tourn., and to Hispania as habitat. It is represented in the Hort. Cliff. herbarium by a specimen labelled with the Tournefort name, though *sericeis* is misspelt *cerisiis*, and in herb. Tournefort by no. 1289. Both are the Spanish plant usually and rightly called *M. supinum* Linn. In Sp. Pl. Linnæus repeats for his no. 4 *supinum* what had been said in Hort. Cliff., with the omission of the Tournefort synonym and the addition of Gallia Narbonensis to the habitat.

There cannot be the slightest doubt about the identity of the species, though it was misunderstood by Scopoli, who took *M. incanum* for it, leading to the erroneous addition of Carniola to the habitat in Willd. Sp. Pl. iii. p. 111. It is strange that Bentham, Lab. p. 742, should not have known the plant and suspected Linnæus to have been describing a garden hybrid. He cannot have looked at the Hort. Cliff. specimen. This mistake he corrected in DC. Prodr. xii. p. 450, but meanwhile it had led Boissier, Voy. ii. p. 509, to substitute the name *sericeum* for *supinum*. Boissier also hesitated on account of the inclusion in the habitat of Gallia Narbonensis, where the species does not grow, and of the citation of Barr. Ic. 686, which he thought "s'applique à une espèce toute différente," without saying to what species. These suspicions are quite unfounded. Gallia Narbonensis is obviously a mistake, and Barr. 686 really resembles Boissier's own figure cxlviii. more closely than does Barr. 685. Indeed Rouy, Exc. Bot. en 1881 et 1882, p. 80 (1883), in distinguishing three varieties of *supinum* quotes Barr. 686 for his var. *Boissieri* and 685 for his var. *Barrelieri*.

The only trouble (of which Boissier was unaware) is about sheet no. 8 Herb. Linn. which is labelled "*supinum* 7." It is an old Hort. Cliff. sheet with the flower-pot design, but *supinum* must be a slip of the pen, for the specimen is not *supinum* and that name does not correspond to no. 7, which both in Hort. Cliff. and in Herb. Sp. Pl. is *M. hispanicum* Linn. The specimen, which is *sine loco*, will not do either for no. 7 or for *supinum*, being in fact the Italian and Dalmatian *Ballota rupestris* Vis.=*B. italica* Benth., and is referred to in Bentham's footnote to *B. italica* in DC. Prodr. xii. p. 519. This unfortunate specimen no doubt played its part in Bentham's earlier confusion of his eastern *B. italica* with his western *B. hirsuta*. There is only one scrap of true *supinum* in Herb. Linn. It lies unrecognised on sheet no. 3 alongside of a good example of *M. incanum*, which has been mentioned in my note on *M. candidissimum*.

## V.

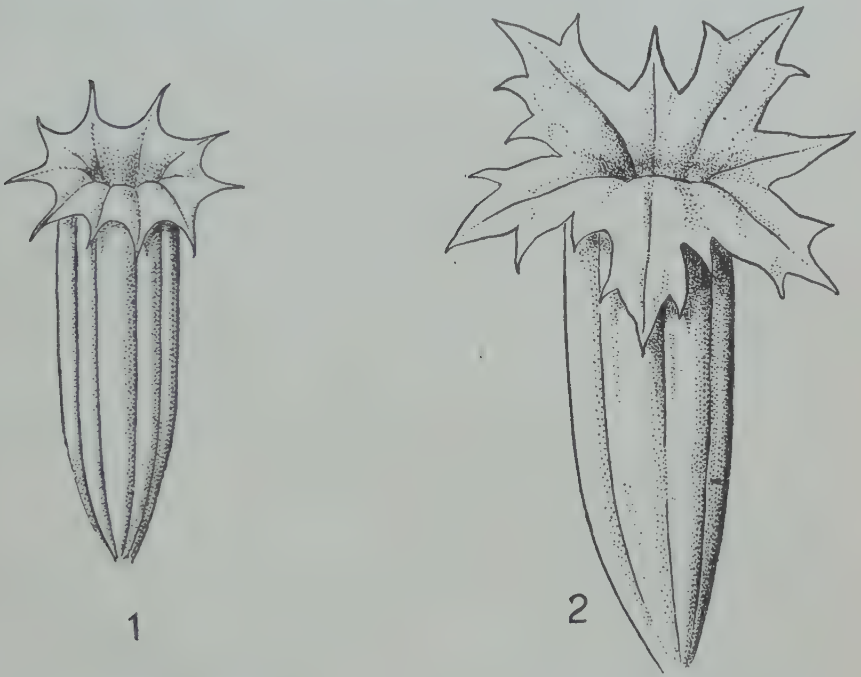
### MARRUBIUM HISPANICUM—BALLOTA HISPANICA—BALLOTA HIRSUTA.

*Marrubium hispanicum*, placed by Linnæus among those "calycibus 10-dentatis," and subsequently transferred to the genus *Ballota*, will involve us in a tiresome discussion of the nomenclature of two very different plants, a Spanish and North African species usually known as *Ballota hirsuta* Benth., and another that inhabits both sides of the Adriatic, commonly called *Ballota rupestris* Vis. The accompanying figure displays the striking difference in their calyces. The conclusion will be that all the current names must be abandoned; that Linnæus's name belongs exclusively to the Spanish species, for which it must therefore be retained as *Ballota hispanica* (Linn.) nobis, non Benth., while the Italian plant should be called *Ballota hirsuta* (Willd.) Kerner, non Benth.

The Linnean name has been the subject of almost incredible confusion between the Spanish species, which does not extend to the central and eastern Mediterranean, and the Adriatic or Italian one that does not grow in Spain. That *Marrubium hispanicum* of the Sp. Pl. really is the Spanish kind, is conclusively proved by: (1) the diagnosis and observation, "calycum limbis patentibus, denticulus acutis . . . . calycis limbo glabro, angulis 10 acutis," which are inapplicable to the Italian plant; (2) the reference to Hort. Ups. p. 169, where it is said that compared with *M. Pseudo-Dictamnus* "calyx in hac magis stellatus et plicatus dentibus acutis," a remark that would not be true of the Italian kind; (3) the quotation of *M. subrotundo folio* Barr. and his Ic. 767; (4) the twice repeated "habitat in Hispania"; (5) the unmistakable specimen of the Spanish species from Hort. Ups. on sheet no. 9 in Herb. Linn., labelled "*hispanicum*" by Linnæus himself.

The only possible objections are: (*a*) the quotation of Herm. Par. tab. 201 (1705), a figure which, although referred by some authors to the Spanish species, to my eye represents very clearly the Italian one. This is borne out by the language in which Hermann differentiates his *M. album rotundifolium Hispanicum maximum* Schol. Bot. Par., of course a garden plant, from *Ocymastrum Valentinum* Clus. This quotation, however, only amounts to the insertion by Linnæus of one mistaken synonym in his otherwise perfectly consistent account of the Spanish *Marrubium hispanicum.* (*b*) The presence of four Hort. Cliff. specimens—three of them in Herb. Hort. Cliff. and the fourth in Herb. Linn. sheet no. 8,—which are the Italian species. Now, although at the beginning of this series of *Marrubium* notes I have pointed out the greater importance of Hort. Cliff. specimens in the genus, this instance forms an exception. They cannot prevail where they are in such flat contradiction with diagnosis and habitat, while the Linnean specimen, sheet no. 9, agrees. The peculiarity of sheet no. 8 has already been explained under *Marrubium supinum.*

Figs. 1 & 2.



1. ***Marrubium hirsutum*** Willd.
***Ballota hispanica*** Benth.; ***B. italica*** Benth.
The Italian species, enlarged about ×7.

2. ***Marrubium hispanicum*** Linn.
***Ballota hirsuta*** Benth.
The Spanish species, enlarged about ×8.

The Spanish plant first appears in Clusius, Rar. Stirp. Hisp. p. 392 (1576), where it is well figured under the name of *Ocymastron Valentinum*; Barrelier afterwards pictured it as *Marrubium hisp. rotundifol. album majus seu latifoliū.*, fig. 767, copied as usual by Boccone, Mus. tab. 122. Brotero, Phytogr. tab. 110, and Hoffmg. & Link, tab. 8 show admirable figures of *Marrubium cinereum* Desr., which is so closely allied as to be treated by Willkomm in

Prodr. Fl. Hisp. ii. p. 446 as identical, and by Bentham, Lab. p. 596, and Rouy, Scrinia fasc. xi. p. 259, as var. *hispida* Benth., though kept up as a species by Coutinho, Fl. Port. p. 251, as *B. cinerea* Briq.

The name *Marrubium hispanicum* has been correctly applied by Willdenow, Sp. Pl. iii. p. 113 (1800), by Desfontaines, Fl. Atl. ii. p. 23, also of 1800 *. On the other hand it has been misapplied to the Italian species by Petagna, Inst. iii. p. 816 (1787), by Sprengel, Syst. Veg. ii. p. 740 (1825), by Gussone, Fl. Sic. Prodr. ii. p. 106 (1828), by Tenore, Syll. p. 292 (1831), and by Host, Fl. Austr. ii. p. 173, in the same year (1831), and notoriously by Bentham, *loc. cit.* (1834), where after a good description of the Italian plant, Spain is erroneously included with Sicily, Italy, and Dalmatia in the *habitat*, while the Spanish plant is also well described, but under the name of *Ballota hirsuta,* on the false assumption—though marked with a query—that it is the *Marrubium hirsutum* of Willdenow, Sp. Pl. iii. p. 113. Some time, however, after the publication of the Lab. Gen. et Spec. Bentham visited Berlin, and discovered that *M. hirsutum* of Herb. Willdenow, no. 10923, is not the Spanish but the Italian kind. See his "Herb. Willd. Didynam. Gymnosperm. cum monogr. Benth. comparatum" in Linnæa, xi. p. 337 (1837). The consequence of this discovery and of the remarks of Gussone in Fl. Sic. Syn. ii. p. 83 (1843) was that in DC. Prodr. xii. (1848) Bentham altered the name of his *Ballota hispanica* to *Ballota italica*, cutting out Spain from the habitat. His new and most appropriate name came too late, for in the preceding year Visiani had already transferred Bivona's *Marrubium rupestre* of 1814 to the genus *Ballota.* Unfortunately Bentham failed to complete his correction by abandoning his name *B. hirsuta* for the Spanish plant, and transferring to it the name *B. hispanica*, as he had better have done.

It must accordingly be taken as established that Willdenow's *hirsutum,* although he did not know its origin, is the Italian plant. This, as pointed out by Visiani, *loc. cit.*, is obvious from the distinctions he draws between *M. hirsutum* "calycum dentibus patentibus lanceolatis," and *M. hispanicum* "calycum limbis patentibus, dentibus ovatis mucronatis," which admirably expresses the distinction so clearly shown in the figures herewith, it is confirmed by Bentham's inspection of the herbarium specimen. The conclusion is therefore irresistible that the name *Ballota hirsuta* must be abandoned for the Spanish plant, and adopted for the Italian species in preference to *B. saxatilis* based on *Marrubium saxatile* Raf. (1814), and to *B. rupestris* based on *M. rupestre* Biv. of the same year, but later, because Bivona quotes Rafinesque's name, or to *B. italica* Benth.

It remains to inquire how so great a botanist as Bentham could have fallen into the two errors of (1) supposing that Linnæus's name *hispanicum* and its diagnosis belonged to the Italian species, and (2) fancying that the Italian species grew in Spain also. There were, in fact, several traps laid for him. As to (1), there was the presence of no less than three Hort. Cliff. specimens —though not actually referred to by Bentham—labelled respectively (a) "*Pseudodictamnus Hispanicus foliis amplissimis, nigricantibus et villosis*, (b) *Pseudodictamnus Scrophulariæ folio*, and (c) *Pseudodictamnus Hispanicus amplissimo folio candicante et villoso*, all of which are Tournefort synonyms quoted in Hort. Cliff., but omitted in Sp. Pl., for *Marrubium calycum limbis patentibus, denticulis acutis*. It is of no concern to us whether the Tournefort synonyms were rightly affixed to these, or not; the important point is that all three are the Italian (or Dalmatian) species. There is no example of the Spanish *hispanicum* in Herb. Hort. Cliff. Then there is the other sheet in Herb. Linn. no. 8, already described under *M. supinum*, which, although so labelled, carries a specimen identical with the last-mentioned three of Hort. Cliff., whence it came. This is referred to by Bentham in DC. Prodr. xii. p. 519 in his note to *B. italica*. Moreover, in Herb. Banks he had seen a Chelsea-garden specimen, no. 2630 of the year 1774, labelled *M. hispanicum*, which is obviously the Italian kind.

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* *M. hispanicum* Desr. in Dict. Encyc. iii. p. 719 (1789) is rather ambiguous, but the description of the calyx seems drawn from the Italian plant as grown at Paris.

As to (2), his unfortunate quotation of Hispania among the habitats of *B. italica* no doubt was due to the presence in Herb. Banks of another sheet of undoubted "*italica*," labelled *M. hispanicum* and *a tergo*, "Spain, ex herb. Pavon." Now it may be that the specimens came from Herb. Pavon, but it never grew in Spain, where the species has never been seen in later times, and where it is against all geographical probability that it should occur. Thus Bentham's error, if not justified, is at any rate explained.

It is unlucky that Bentham's misuse of the name *Ballota hispanica* should have been an obstacle hitherto to its correct employment for the Spanish species. The following chronological synonymy avoids disturbing *B. saxatilis* Sieber ex Benth. (1834), which might have to give way if Willdenow's name is not accepted for the Italian plant, for which *M. saxatile* Raf. is the next earlier specific.

*For the Spanish species.*

BALLOTA HISPANICA nobis, 1925.
*Marrubium hispanicum* Linn. 1753.
*Berlingera hispanica* Neck. 1790.
*Marrubium hispanicum* Willd. 1800.
,, ,, Desf. 1800.
,, *cinereum* p. pte., Spreng, 1825.
*Ballota hirsuta* Benth. 1834.

*For the Italian species.*

BALLOTA HIRSUTA Kerner, 1884.
*Marrubium hirsutum* Willd. 1800.
,, *saxatile* Raf. 1814.
,, *rupestre* Biv. 1814 (later).
,, *hispanicum* Spreng. 1825.
,, ,, Guss. 1826.
,, *hirsutum* Reichb. 1830.
,, *hispanicum* Ten. 1831.
,, ,, Host, 1831.
*Ballota hispanica* Benth. 1834.
,, *saxatilis* Guss. 1842.
,, *rupestris* Vis. 1847.
,, *italica* Benth. 1848.
*Berlingera hirsuta* Nym. 1854.
*Ballota hirsuta* Halácsy, 1902.

If it should be thought that Kerner's *Ballota hirsuta* is inadmissible owing to his mistaken quotation of *B. hirsuta* Benth. as identical, the name would still prevail, but be attributed to Halácsy, as above.

If *Berlingera* were to be kept up as a genus, all the trouble would be avoided. We should have *Berlingera hispanica* Neck. (1790) and *Berlingera hirsuta* Nym. (1854).

## VI.

### MARRUBIUM CIRCINNATUM.

*Marrubium circinnatum* Desr. in Dict. Encyc. iii. p. 217 (1789) was described from a single specimen in Herb. Jussieu. Bentham, in Lab. p. 592 and in DC. Prodr. xii. p. 454, treats this species as "*non satis nota*," merely transcribing Desrousseaux's description. Boissier, in Fl. Or. iv. p. 702, more rashly identifies it with *M. velutinum* Sibth. et Sm. Evidently neither of them had inspected the type which still lies in Herb. Jussieu at the Paris Museum, under no. 5578, labelled "*Marrubium album foliis amplis fere circinnatis*," without any indication of origin. It is obvious at a glance that the plant is not *M. velutinum* but *M. rotundifolium* Boiss., Diagn. ser. 1, 5, p. 33 (1844). The characters by which *rotundifolium* is distinguished from *velutinum* by Boissier, *loc. cit.*, and in Fl. Or. iv. p. 698, are conspicuous in Jussieu's specimen, which agrees with those collected on Mount Sipylus in Lydia by Balansa, Pl. d'Orient, 1854, no. 329, and by Bornmüller in 1906, no. 9905, as well as on M. Tmolus above Philadelphia by Boissier himself. Herb. Banks in Mus. Brit. contains a specimen labelled "*Marrubium folio subrotundo* Bocc., a D. Sherard 1719" which is identical with the plant in Herb. Juss., and of course should not bear Boccone's name, which belongs to *M. supinum* Linn.

Tournefort is very likely to have met with *M. circinnatum* on M. Sipylus on the 17th December, 1701: "nous nous amusâmes ce jour là à herboriser sur le Mont Sipylus" (Voyage, ii. p. 492). This record induces me to think that *M. album incanum candidissimum et villosum* was very possibly *M. circinnatum*. Though it would not have been in flower in December, which might account for the absence of a specimen in Herb. Tourn., he may have brought home plants which afterwards furnished the specimens of Jussieu and of Sherard.

## VII.

### MARRUBIUM in Herb. Tournefort.

The seven species of *Marrubium* enumerated in the 'Institutiones,' pp. 192, 193, are European; the remaining four, which are Oriental, are mentioned in the 'Corollarium,' p. 12. It may some day be of use to a monographer of the genus to record which of these are represented in Tournefort's herbarium at the Paris Museum.

1. *M. album vulgare* C. B. P. is represented in the herbarium by sheet no. 1284, which bears no label.

2. *M. album villosum* C. B. P., so labelled on sheet 1283, is the form of *vulgare* that corresponds to *M. apulum* Ten.

3. *M. album latifolium peregrinum* C. B. P., so labelled on sheet 1285, is *M. incanum* Desr. = *M. candidissimum* auct. non Linn.

4. *M. album peregrinum, brevibus et obtusis foliis* C. B. P., with syn. *M. creticum angustis foliis inodorum* Eyst., is not represented in the herbarium.

5. *M. album angustifolium* C. B. P., with syns. *M. album angustiore folio* J. B. and *M. creticum* Tab., is represented by two identical specimens, nos. 1287 and 1288. These have broadish leaves, a large spreading panicle, and more than 5 calyx-teeth. They are *M. paniculatum* Desr. = *M. remotum* Kit.; they do not therefore seem to agree with the name.

6. *M. hispanicum supinum calyce stellato et aculeato* with syn. *Alyssum Galeni* Clus. is obviously represented by sheet 1286, though unlabelled. The specimen is *M. Alysson* Linn.

7. *M. hispanicum supinum, foliis sericeis argenteis* with syn. *M. album sericeo parvo et rotundo folio* Bocc. is represented by sheet 1289, labelled *Marrubium d'Espagne* and *Marrubium hispanicum sericeum incanum Alysso Clusii congener, flore purpurascente.* It is *M. supinum* Linn.

8. *M. album candidissimum et villosum.* This is undoubtedly the name for an Oriental species, like other names in the 'Corollarium.' It is unidentifiable, because not really represented in the herbarium, although on the label to sheet 1290 we read *Marrubium album græcum foliis ad basin acutis*; *M. album candidissimum et villosum* Coroll. Inst. But both this no. 1290 and the similar unlabelled 1291 are just forms of *M. vulgare*, with upper stem-leaves not cordate or rounded at the base but tapering into the petiole. They both have the characteristic ten-hooked calyx-teeth of *vulgare*. The label may have been accidentally attached to a wrong sheet, or, if Tournefort meant to call these specimens *M. album græcum foliis ad basin acutis*, which is not improbable, the synonym *M. album candidissimum et villosum* has been added by an oversight of his own or of some other person who wrote the label.

9. *M. Orientale, foliis subrotundis, flore purpureo. Idem flore albido.* Sheet 1292, labelled *M. cappadocicum, foliis subrotundis flore purpureo*, corresponds to this and is *M. astracanicum* Jacq., as has long been recognised. No. 1293 bears a similar label with *flore albo* instead of *flore purpureo.* There is another Tournefort specimen of each of these in Herb. Banks at the British Museum; they were used by Bentham for his description of *M. astracanicum.* In Herb. Jussieu there lies a pretty woodcut, *ic. ined.*, of one of these or of a similar specimen with the legend *M. orientale foliis subrohendis* (sic) *flore purpureo.*

10. *M. Orientale angustissimo folio flore albo* is not represented in the herbarium.

11. *M. Orientale, Catariæ folio, flore albo* represented by sheet 1294, which is labelled *M. ibericum, Catariæ folio, flore albo*, is *M. catariæfolium* Desr., as pointed out by Boissier in Fl. Or. iv. p. 700. There is another Tournefort example of this in Herb. Banks.

It will be noticed that species 4 and 10 are not found in the herbarium, that the specimen for no. 5 does not exactly correspond to the name, and that for no. 8 not at all.

## EXPLANATION OF THE PLATES.

### Plate 2.

*Marrubium folio candidissimo orbiculare, crassissima*, from the Cliffordian Herbarium, in the British Museum (Natural History).

### Plate 3.

*Marrubium folio rotundo candidissimo*, from the Cliffordian Herbarium.

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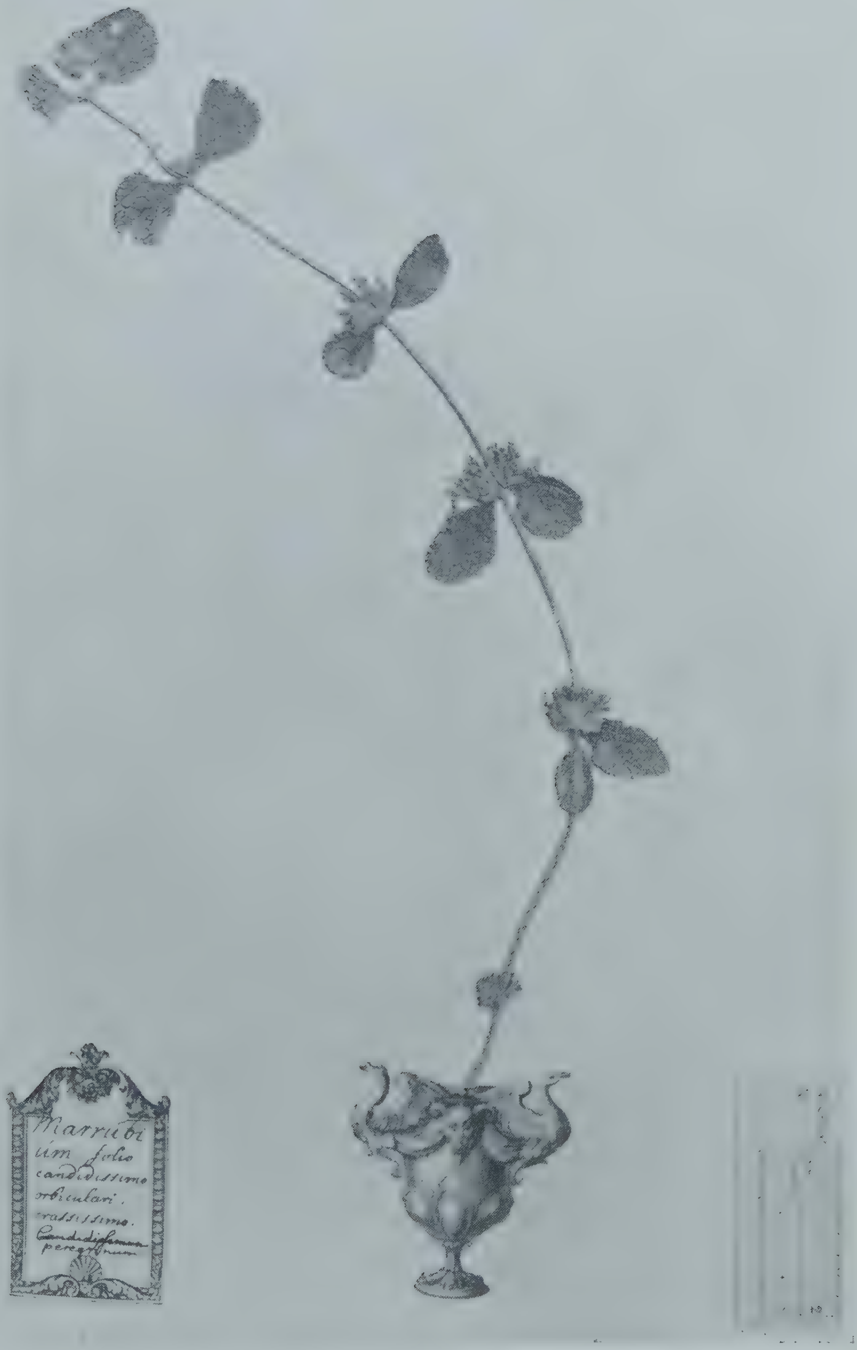
## Colchicum montanum.

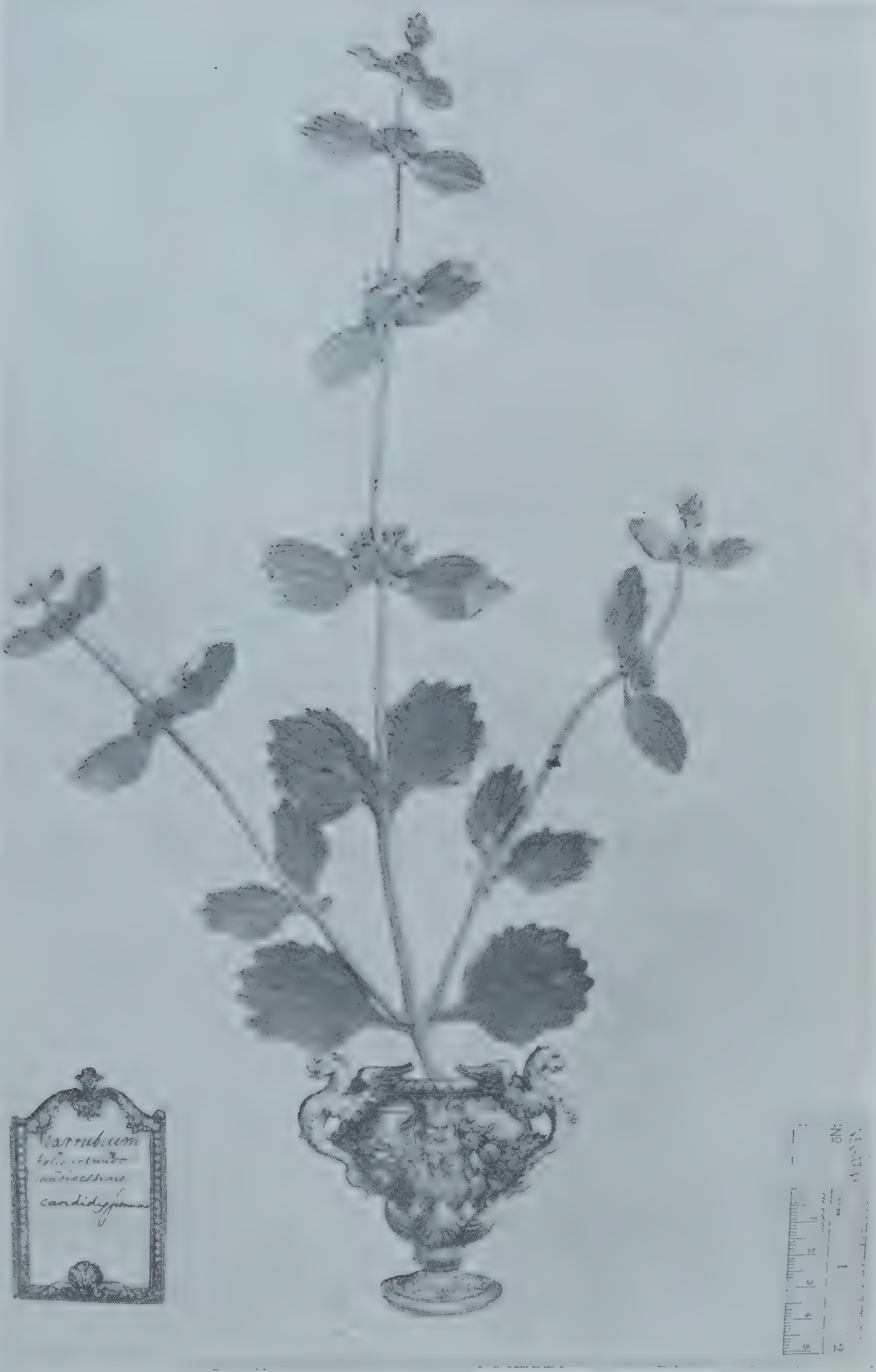
This is a name that must be abandoned. It is a striking instance of the confusions that abound in 'Species Plantarum,' where *C. montanum* is a mixture of *Merendera Bulbocodium* Ram. from the Pyrenees and Spain with *Colchicum alpinum* DC. from the Alps and northern Apennines. Neither bears any resemblance to *Colchicum Bertolonii* Stev., the common synanthous-leaved *Colchicum* of Italy, to which name *C. montanum* Linn. has so often been wrongly applied.

Linnæus does not himself describe *C. montanum*, but merely quotes Loefling's diagnosis, "*Colchicum foliis linearibus patentissimis*," and two synonyms, *C. montanum angustifolium* Bauh. Pin. and *C. montanum* Clus., with Hispania et Helvetia as habitat. Now the plant described and figured by Clusius, Rar. Stirp. Hisp. p. 266, was found by him on the stony hills near Salamanca, where he says it was called *Merenderas* or *Quitameriendas*. This is notoriously *Merendera Bulbocodium* Ram. = *Merendera montana* Lange, and is the very same plant that Loefling saw plentifully in the plains of Estremadura and Castile on his journey from Lisbon to Madrid in October 1751, though he did not attempt to distinguish it generically from *Colchicum*. See his letter to Linnæus of Nov. 1, 1751, in his Reise, p. 26. All this was indicated long ago by Lapeyrouse, Hist. Pyr. p. 201 (1813), and has been accepted by Willkomm & Lange and by Parlatore. Then the Bauhin synonym, which accounts for the "habitat in Helvetia," is admittedly *C. alpinum* DC., Fl. Fr. iii. p. 195 (1805), where—by the way—the name *C. montanum* is misused.

We cannot adopt the name *C. montanum* Linn. for Clusius and Loefling's Spanish plant, except by transferring it to the genus *Merendera*, as Lange has done, to replace *Merendera Bulbocodium*. On the other hand we must



MARRUBIUM GLOBOSUM No. 1.

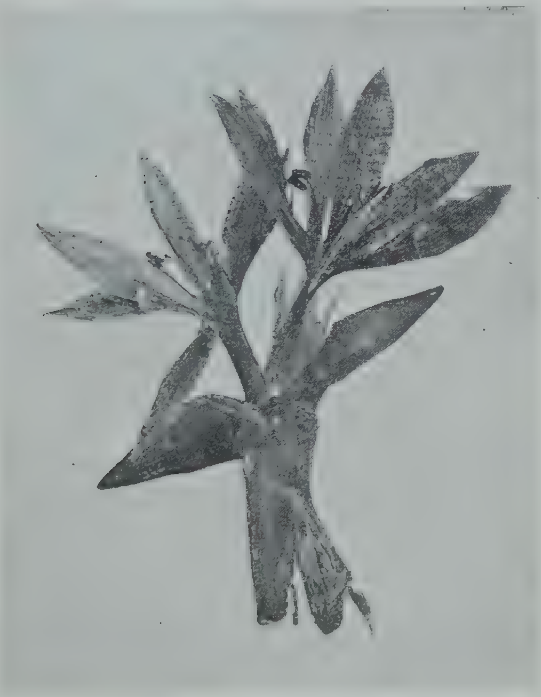


MARRUBIUM GLOBOSUM No. 2.

not say "*C. montanum* Linn. is *C. alpinum* DC.," because the diagnosis, such as it is, was intended by Loefling for the Spanish *Merendera* and not for any *Colchicum*. Nor can we say that *C. montanum* is the plant that lies in the herbarium under this name, because the specimen though a *Colchicum* is not *C. alpinum*, nor, of course, *Merendera*, and therefore conflicts with the text of 'Species Plantarum.' Consequently the name must be rejected altogether as *nomen confusum*.

The herbarium specimen marked by Linnæus *Colchicum montanum* is unmistakably *C. bulbocodioides* Bieb., which replaces *C. Bertolonii* as we go east, and is specifically distinguished by much broader leaves, by 10–20-nerved instead of 5–7-nerved tepals, and by its different flowering season, which is from March to May according to the altitude, instead of from September to November. See Boiss. Fl. Or. v. p. 164 (1884) and Halácsy, Comp. Fl. Gr. iii. p. 274 (1904). It is strange that this specimen, in which the characters of *bulbocodioides* are very evident, as may be seen even from the accompanying photograph, should have been misapprehended by all the authors who refer to it. Smith wrote on the sheet, after the words *Colchicum montanum*, "minime; an *Bulbocodium vernum*? J. E. S.," though the style

FIG. 3.



*Colchicum montanum*, Herb. Linn. Natural size.

shows that it cannot be a *Bulbocodium* and the anthers that it is not a *Merendera*; both organs are visible and are those of a *Colchicum*. Ascherson and Graebner, Syn. iii. p. 20, quote this specimen for *C. Bertolonii*, which it certainly is not. Bertoloni, Fl. It. iv. p. 277 (1839), says under his *montanum*, which is *Bertolonii* Stev., that "Archetypus hujus speciei ex observationibus Gussonii desideratur in herbario Linnaeno," an astounding statement to come from such a precisian as Gussone, who had himself dipped into the Linnean herbarium. But when that author says, in Fl. Sic. Syn. i. p. 437 (1872), "in herb. Linn. species hæc desideratur," he may only mean that the plant he was at the time describing, which he calls *C. Cupani*, is not to be found in the herbarium: as is the case. On the other hand Visiani, Fl. Dalm. Suppl. p. 36 (1872), and Baker, in Journ. Linn. Soc, Bot. xvii. p. 433 (1879), both attest the existence of the specimen of "*C. montanum*," but the former falls into the error of identifying it with *C. Bertolonii*, while Baker complicates matters, for he identifies *C. bulbocodioides* with *C. montanum* in the sense of *C. Bertolonii*. He was probably unaware of the difference in flowering season, and cannot have noticed the other characters subsequently pointed out so clearly by Boissier and by Halácsy. Then he made a grave mistake in assuming the specimen to be one received by Linnæus from Loefling. Of this there is not a shadow of evidence, and three considerations make it impossible: (1) if it were Loefling's example it would be *Merendera* and not *Colchicum*; (2) it is not like any plant that grows in Spain, where the very distinct *C. triphyllum* Kuntze is the only *Colchicum* besides *C. autumnale*; (3) although there is no indication of origin on the face of the sheet, there is written on the back by Linnæus, "habitat in Morea."

Thus it appears that there is no connection of any sort between this specimen and the *C. montanum* of the 'Species Plantarum,' nor indeed would there be any had the example chanced to be really *C. Bertolonii* instead of *C. bulbocodioides*. We cannot, on the strength of the specimen, follow Boissier, *loc. cit.*, in using the Linnean name as equivalent to *C. bulbocodioides* Bieb., for the herbarium cannot take precedence of the 'Species Plantarum' when there is disagreement. Ascherson and Graebner have unfortunately adopted the same course as Boissier.

I have dealt in more detail with the name *Colchicum montanum* in a recent paper in Nuov. Giorn. Bot. It. xxxii. (1925), being no. ci. of my "Piante italiane critiche o rare." I venture to express the opinion that Linnæus never saw a specimen from Loefling. Had he seen one we may feel sure that he would not have admitted it as a *Colchicum*. The Linnean Society has a MS. list (Box xvi. no. 7) *manu ignota* of a "Herbarium Loeflingianum; Matriti" in which *Colchicum montanum* occupies no. 176, but Dr. A. Caballero writes from Madrid that he is unable to trace the existence of such a herbarium there at the present day.

# Two Rare Spanish Species of *Echium*.

By C. C. Lacaita, M.A., F.L.S.

(Plate 4.)

[Read 5th March, 1925.]

Echium marianum and Echium Pavonianum are only known from single specimens in Herb. Boissier ; through the kindness of M. Beauverd, the keeper of that herbarium, I am able to show a photograph of these, both placed on one sheet for economy of space.

*E. marianum.*—This specimen was referred by De Candolle in Prodr. x. p. 16 (1846) to *E. fastuosum* (Jacq. f.), but wrongly, as pointed out by Boissier, who published his name of *E. marianum* in Diagn. Pl. Or. 11, p. 90 (1849). The specimen itself came to him from Dr. Prolongo, of Malaga, who is supposed to have gathered a single individual in the gorges of the Sierra Morena near the Madrid road in the company of *Digitalis mariana.* The label reads :

> "E. marianum Boiss. ined. in rupibus montis Mariani (Sierra Morena) a cl. Pabl. Prolongo Malacensi collect."

No trace of the plant has ever again been seen by those botanists who have occasionally visited the famous gorge of Despeñaperros. On June 26th of this year, 1925, I followed the Madrid road right across the Sierra from Santa Elena to Venta de Cardenas, without discovering any sign of the presence of this species. It is to be feared that the label became attached to a wrong plant, before the specimen came into Boissier's possession. It is impossible in such a case to prove a negative, but for the present *Echium marianum* must be excluded from the flora of Spain.

The case of *E. Pavonianum* is more difficult. The label of this specimen, which came from Herb. Pavon, states that it grew at Aldeguela, and was most abundant there in September 1806, so it should not be difficult to rediscover the plant if we knew what village is meant by "Aldeguela." Unfortunately there is no place in Spain of that name, as De Candolle, *loc. cit.*, remarks in a note: "Aldeguela in lexicis geographicis deest et origo non certe hispanica." Boissier, on the other hand, says "Hic locus mihi ignotus est sed ex schedulæ formâ comparatione in provinciâ *Extremadurâ* probabiliter situs." Now, although there may be no such place as Aldeguela, the Spanish gazetteer records no less than 33 of the very similar name of Aldehuela, a word which literally means "hamlet." Of these, three are in Estremadura and three more in the adjacent province of Salamanca. I have been close to Aldehuela de la Boveda and Aldehuela de Yeltes in the latter district; both lie in cultivated land where the presence of such an *Echium* is very improbable, and if it grows most abundantly one could hardly overlook it.

As to the three Aldehuelas in Estremadura; the same remark applies to the one which I have visited—I do not think any one else has been there—on the right bank of the river Jerte, some 10 miles S.W. of Plasencia. Another is in a remote part of the Hurdes, the wildest and most inaccessible corner of Spain; it is described in an old gazetteer as lying at the foot of the Puerto de Esparaban, and consisting of 25 cabins (in the Irish meaning of that word). It is incredible that Pavon should have visited such a spot, which even to-day is some 30 miles by rough mountain tracks from the nearest highroad. I penetrated some distance into the Hurdes, from the old deserted monastery in the lovely glen of Las Batuecas, but did not get within 12 miles of Aldehuela. The flora of these grim hills of the Hurdes seems to be extremely poor and very uniform, being mostly composed of sundry species of *Erica* and *Cistus* or *Halimum* mixed with *Arbutus Unedo*. There is an interesting account of this very little known district in Aubrey Bell's 'Pilgrim in Spain' (1924).

I could not find time to visit the third Aldehuela in Estremadura, which is more accessible, lying not far from Caceres. This one offers the best, if not the only, hope of rediscovering Pavon's plant, but I confess to some scepticism as to its existence in Spain; the habitats assigned in Pavon's labels are not always to be trusted. Witness the case of *Marrubium hispanicum* ex Herb. Pavon in Mus. Brit. mentioned in my recent paper on *Marrubium* and *Ballota* in this Journal (*supra*, p. 169).

The label of *E. Pavonianum* reads:

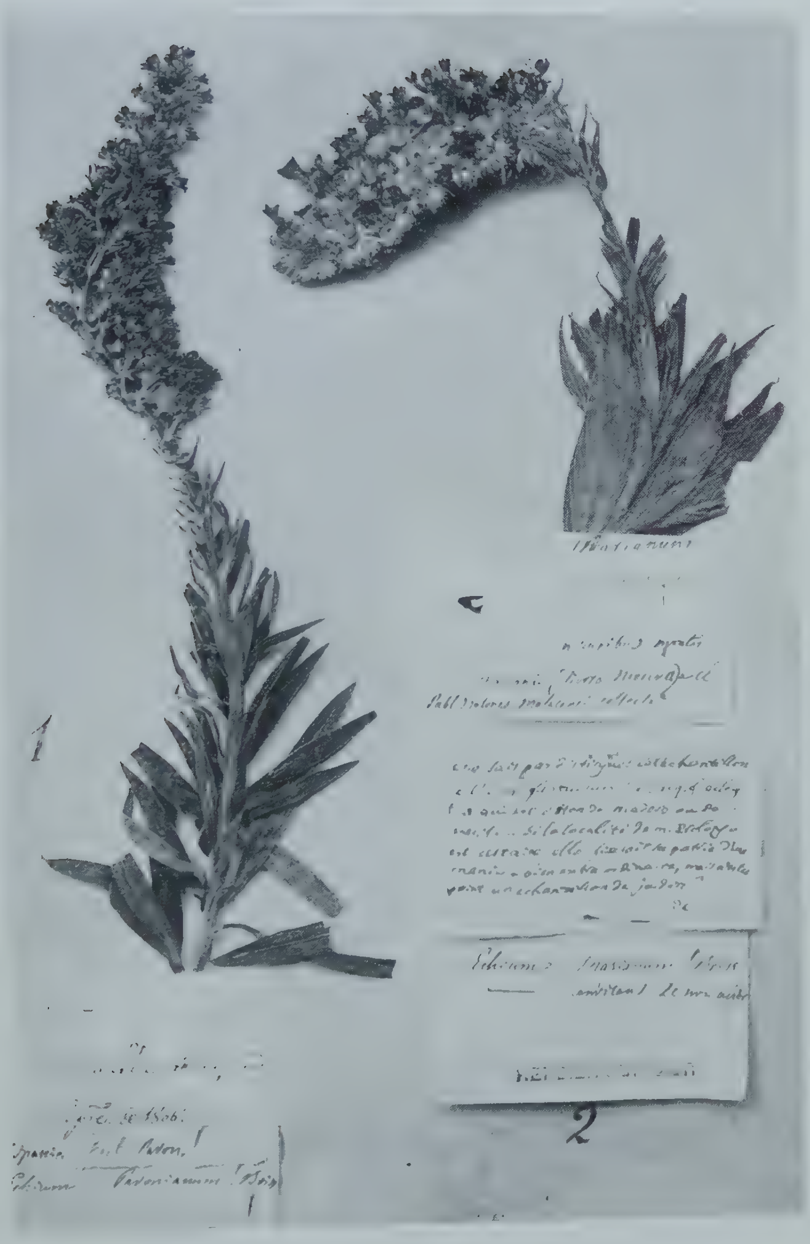
> "Echium
> Aldeguela abundantis$^{\text{mo}}$.
> Sepr̂e de 1806
> Hispania. Herb. Pavon."

## EXPLANATION OF PLATE 4.

Fig. 1. *Echium Pavonianum* Boiss.

Fig. 2. *Echium marianum* Boiss.

Both from photographs by M. Beauverd, Herb. Boissier.



TWO RARE SPANISH SPECIES OF ECHIUM.

# The Male Organs of the Florideæ. By VIOLET M. GRUBB, M.Sc.
(Communicated by Dr. E. MARION DELF, F.L.S.)

(With 36 Text-figures.)

[Read 4th December, 1924.]

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## I. Historical Account.

ALTHOUGH nearly 150 years have passed since the first record of spermatia in the red algæ occurred in print, our knowledge of these minute bodies which play so important a part in the reproductive processes of the Rhodophyceæ is surprisingly inadequate and limited. Records of the observation of antheridia in more than 120 European species of the Florideæ are to be found scattered in algal literature, but of these the vast majority are simply notes to the effect that male plants have been seen and recognized. A certain number give a short description detailing the position of the antheridia, and some include a slight account of their structure, but owing to the nature of the material, modern cytological methods of investigation have only been brought to bear on a few forms. Where, however, such methods have been tried the results have well repaid the labour, nothing being more striking than the remarkable uniformity shown by the antheridia in their development. At the same time their structure has thrown interesting light on the question of systematic relationships, since these have so far been mainly determined on the characters of the cystocarpic and tetrasporic plants.

The first mention in literature of the antheridia of the red algæ occurs in a letter from John Ellis, Esq., F.R.S., to Dr. Linnæus, F.R.S., of Upsala, written in 1767. The main subject of the letter purports to show the animal nature of the genus of zoophytes called *Corallina*, but it includes an account of "some remarkable discoveries in the year 1754 on the coast of Sussex"; these were the supposedly male and female fructifications of *Conferva polymorpha* Linn. and *Conferva plumosa* Ellis (now known as *Polysiphonia fastigiata* Grev. and *Heterosiphonia coccinea* Falkenb. respectively), the male showing "its amentaceous flowers or catkins, with its minute male seed in spikes." On the ground of the presence of these fructifications, Ellis recommended that *Conferva* should be included in Linnæus's class of Diœcia. Ten years later Lightfoot (1777) repeated this observation on *Conferva polymorpha*, again insisting from analogy with Angiosperms that the "small conic catkins" were male in character, though knowing nothing of their true function. In the next thirty years these observations were extended to other species of *Polysiphonia* by Roth (1797), Lyngbye (1819), and Bonnemaison (1822, 1828), who added nothing new as regards the function of these bodies; indeed, the first two authors rather obscured the issues by suggesting that these "catkins" were really of animal origin; and although this was not accepted by Agardh (1828) in his notes on the five species of *Hutchinsia* Ag. (*Polysiphonia* Grev.), in which he had observed antheridia, yet he acknowledges that their function is unknown. Two years later Greville (1830) was much puzzled by the discovery of yellow bodies on the upper branches of *Rhodomela pinastroides* Ag. "resembling what are called anthers in the Jungermanniæ," but came to the conclusion that these were "certainly extraneous and probably of animal nature." At the same time he saw capsules or cavities terminating the branches in *Laurencia pinnatifida* Lamour. filled with "extraordinary bodies"; these were also seen by Mrs. Griffiths in some Cornish specimens, but no explanation of them was found. Kützing (1843) noted the structures in *Wrangelia*, species of *Polysiphonia*, and in *Odonthalia dentata* Lyngb.

under the name of "spermatodia," and added two observations of importance, one being that, wherever these occurred, no other fruit-body was found on the same individual, and the other that the gonidia composing the "spermatodien" were colourless and homogeneous. Naegeli (1847) revived the question as to what was the function of these bodies, comparing them with the antheridia of mosses and liverworts, but unfortunately suggesting by this comparison that the corpuscles liberated were motile, as in the Bryophyta, and indeed stating that a spiral cilium could be seen inside the colourless cell. This idea was taken up enthusiastically by Derbes and Solier, who worked it out in many of the 27 species in which they observed antheridia (1850, '56): in most cases more detailed descriptions than had previously been undertaken were given, accompanied by figures, but at the same time these accounts were coloured by the idea that the Floridean "spermatozoids" possess a fine motile terminal appendage. Simultaneously with these papers, others, which were models both for their accuracy and the powers of acute observation to which they gave evidence, were being published by Gustav Thuret on the antheridia of the Cryptogams and more especially of the Florideæ (1851, '55, '78). Altogether this investigator listed 68 species in which he had observed the presence of antheridia, and these, added to the 17 others known previously, makes a total of 85 European species to date. In addition he gave descriptions of a good many of these species, and, as a result of his extensive observations, he came to the conclusion that the hyaline corpuscles which are expelled into the water show no signs of movement, nor can any trace of a filamentous appendage be distinguished: this statement as to the lack of motility in the spermatia of the Florideæ has never since been seriously disputed. Thuret was led early to speculate as to the function of these organs, which appeared to be so widespread, and on the grounds of their position (see p. 240) and frequent occurrence he suggested that they were "organes de fertilisation." This bold suggestion, which at the time did not seem to be justified, was fully borne out by the remarkable announcement made in company with Bornet before the Académie des Sciences on Sept. 10th, 1866, of the fusion of these "corpuscles" of the Florideæ with the tip of the "appareil trichophorique." The good work done by Thuret was carried on by his disciple, Guignard (1889), who published a more detailed account of some of the species already described and added several others. Schmitz, too, in his account of the fertilization of the Florideæ (1883), gives some description of the antheridial bodies, more especially trying to establish the fact that the cells from which the spermatia arise are always terminal in position (see p. 241). During the past fifty years short descriptions of antheridia, too many to enumerate, are found in the accounts of the algal flora of various coasts, as well as in monographs of different genera. But it is to Svedelius and Kylin in the main that we owe the detailed cytological investigations which have been undertaken of several genera, and without which it is impossible to arrive at any clear idea of the exact morphology, development, and structure of the antheridia. With the idea of adding to the number of such facts and so perhaps throwing light on the many obscure problems connected with the male organs, the following investigation and discussion have been undertaken.

## II. Terminology.

Before proceeding to the detailed description of the antheridia in the following fifteen species, it is necessary to explain the nomenclature which will be employed, for the terminology in use with reference to the male organs of the Florideæ is both ill-defined and confused. This is partly due to the fact that when names were first adopted for these organs, their function and structure were not properly understood ; further knowledge has necessitated the modification of the original terms and in some cases the addition of new ones, and as a result there are several systems of terminology in existence for the male organs and the cells subtending them.

The name "antheridium" was first applied by C. A. Agardh (1828, p. 57) to the terminal pedicellate structures visible in *Polysiphonia* Grev. (then known as *Hutchinsia* Ag.) at the apex of the branches. Although it had already been suggested by Ellis (1767) that these "amentaceous flowers" or "catkins" might represent the male organs, the name was not given by Agardh from any true conception as to the function of the bodies, but merely from their close outward resemblance to the anthers of stamens in the Angiosperms. The word antheridium retained this original meaning in the red algæ throughout the works of Derbes and Solier, Thuret, and Buffham, and by all these writers it was regarded as denoting "productions celluleuses incolores, de formes variées, qui se développent à la même place que des organes de la fructification. . . . elles ont toujours pour caractère essentiel d'être composées de très petites cellules hyalines, qui renferme chacune un corpuscule ovoïde ou sphérique, également incolore" (Thuret, Ann. Sc. Nat. 4$^e$ sér. Bot. iii. (1855), pp. 16–17).

Some years later a change occurred in the terminology which had been vaguely foreshadowed by Goebel (1887), for in one place he states that "These *groups* of mother-cells of the spermatia are called antheridia" (p. 73), and in another, speaking of all algæ in general, "The male elements, the mother-cells of which are called antheridia" (p. 6) ; in this second quotation he definitely regards the *single* mother-cell from which the male element or elements issue as the antheridium and not a group of such cells. Guignard a few years later adopted this new use of the term antheridium, applying it in the Florideæ to denote "une petite cellule incolore, dont le contenu est employé tout entier à former un seul pollinide" (1889, p. 175) ; in this sense the word has also been used by Rosenvinge and Oltmanns. If, however, this new terminology is adopted, some name has to be found for the groups or masses of male organs which are developed in many species and were originally known as antheridia; for these the words "Antheridienständen," "Spermatangienständen," or "Gruppen" have been suggested by continental authors, while the term "sorus" has universally been used (Delf and Grubb, 1924, p. 330, note).

Naturally, however, this new application of the term antheridium has not been at once universally adopted, and in the last century Schmitz strongly upheld the use of the word in Agardh's sense to denote a "grösseren oder kleineren Gruppe von Spermatangien und Tragzellen der Spermatangien, soweit sich diese Gruppen selbständig am Thallus der Mutterpflanze abheben" (1893, p. 231, ftnote 2). This meaning of the term is also in use at the present day in the writings of Svedelius (1908, p. 77) and Kylin (1922, p. 121); the latter, however, inserts in most cases the term "Spermatangienstände" as a substitute for "antheridium."

The argument in favour of changing the original meaning of the term antheridium in the red algæ lies in the resemblances which can be drawn between the male organs in this group and similar organs in the brown and green algæ, and the desire to avoid confusion by adopting a single term to denote the same structure in all the algæ. As Oltmanns points out, the word is used in the Phæophyceæ and Chlorophyceæ to describe the single cell from which the male elements or spermatozoids are produced, whether many spermatozoids issue from this mother-cell as in *Dictyota* or *Fucus*, two as in *Cylindrocapsa* and most species of *Œdogonium*, or only a single one as in *Coleochæte pulvinata*. Since the term is already in use in this sense, in the other algal groups it seems unnecessary to add to the already confusing terminology in the Florideæ by applying to the whole group of male organs a word which is well known to bear another meaning, and which in any case was applied to the Florideæ at a time when the function of the male organs was not known, and when, indeed, it was not even realized that these bodies played any part in sexual reproduction. The argument put forward by Svedelius (1908) in favour of retaining the original meaning of the word and calling the cell giving rise to the spermatium, the spermatangium (a word first introduced by Schmitz), is based solely upon the peculiar apical successive constriction of the spermatia in *Martensia*. He contends that this production of spermatia is so entirely different from any known method of spermatozoid development in the green and brown algæ, that it is impossible to apply the term antheridium to the cell giving rise to the male element in both cases. But it must be remembered that the type of construction in *Martensia* as described by Svedelius, is found only, as far as is at present known, in two other cases in the Florideæ (see p. 242), and cannot therefore be regarded as sufficiently typical to form an argument for the retention of the old terminology, or to necessitate the coining of a new term for the single cell such as "spermatangium."

The single colourless bodies which issue from the antheridia are now by general consent known as spermatia. At first no definite name was given to them, and they were simply called "corpuscles" (Derbes and Solier; Thuret and Bornet) or "pollinides" (Guignard and Schmitz). Derbes and Solier, as well as Naegeli, had early suggested that these corpuscles might possibly play some part in sexual reproduction, though not in the least understanding what this part was, and, borrowing a term from the animal kingdom, they propounded that these bodies, which they wrongly regarded as being motile, should be called spermatozoids; it was also suggested that to distinguish them as animal and not plant structures the term should be changed to antherozoids. Thuret pointed out that the antherozoids were not motile, and therefore this term was not strictly applicable, but Goebel was the first to introduce the name spermatium for the body which escaped from the antheridium, and this name was adopted by Schmitz in his later papers (1897), as well as by Oltmanns and all recent writers on the subject. If further evidence in favour of the application of the term antheridium in Guignard's or Oltmanns's sense were needed, it could be found in the peculiar nuclear behaviour of the spermatium. In section VIII. of this paper it is shown that there is reason to suppose that at one time two spermatia were produced from a single antheridium, but that in most cases they have now been reduced to a single one; a similar state of things is found in the genus *Œdogonium*, where, in the majority of species, such as *Œ. crispum* (Hass.) Wittr. and *Œ. Vaucherii* (de Clerc) Ag., two antherozoids are produced from a single antheridial cell, but in others, such as *Œ. curvum* Pringsh. and *Œ. calcarum* Cleve, only one escapes from each cell. None the less, this cell is called an antheridium, and by analogy the mother-cell should equally so be called throughout the Florideæ. When, as in many species of this latter group, a succession of antheridia are formed one within another, these are then known as secondary or tertiary antheridia.

There remains yet another cell concerned in the formation of the spermatia to which a variable terminology has been applied, and this is the cell which subtends the antheridium and from which the latter arises. By Schmitz (1883) it was given the name of "Tragzelle." Svedelius (1908) objects to the term on the ground that it has no particular meaning and substitutes in its place "Spermatangienmutterzelle," and this is also adopted by Kylin. But since the word spermatangium has been rejected for that of antheridium, on the ground of the lack of necessity for the introduction of an entirely new word, it is obvious that the cell from which the antheridium arises must either be known by the name given by Schmitz or else as the antheridial mother-cell. This latter term, though certainly cumbrous, will be adopted here, as being more expressive and less confusing than the introduction of an entirely new word such as "Tragzelle." If, as in some cases, a special vegetative cell is interposed between the antheridial mother-cell and the normal vegetative cells, this is known as the basal cell, though it has also been called by Yamanouchi (1906) the stalk cell.

To sum up, the spermatia, which are colourless hyaline bodies, are, in the higher Florideæ, each borne singly in a cell known as the antheridium, from analogy with the cell containing the male element in other algæ. These antheridia are subtended by another cell known as the antheridial mother-cell, and are frequently clustered together in sori or groups on the surface of the thallus.

## III. **Materials and Methods.**

The material used in the present investigation was gathered mainly on the rocks at Shanklin and Swanage during visits to these places at different times of the year. In addition, a certain number of deep-sea forms, which would otherwise have been inaccessible, were obtained from dredgings carried out at the Plymouth Marine Biological Laboratory by the kindness of the Director, Dr. E. J. Allen, in April 1924. In each case the date when the material was gathered is given with the detailed descriptions.

In the majority of instances it was found that antheridial fronds or thalli could, after careful examination, be recognized on the shore. The prevailing characteristic, revealing the presence of spermatia, is a paleness or whiteness of the frond in the region of the development of these bodies; in some cases, once the appearance is known, this cannot be overlooked (*i. e.* pale sori of *Nitophyllum Hilliæ*): in other instances, recognition is aided by the development of spermatia in special structures (*i. e.* the pale yellow conceptacles of *Laurencia pinnatifida*, or the colourless "leaflets" of *Nitophyllum laceratum*). But in a few species, although the position of the spermatial sori was known, it was found impossible to pick out male from sterile fronds apart from microscopic examination (i. e. *Ceramium rubrum*, *Callithamnion* sp.).

When possible the spermatial material was fixed on the shore in Flemming's weaker solution for algæ. This fixative was found to give the best all-round results, both in preservation without shrinkage of the cytoplasm and chromatophores, and also in detailed structure of the nuclei. The algæ were allowed to remain in the liquid for varying times according to their structure; in the case of delicate filamentous types (*Polysiphonia*, *Ceramium*) 1 to 3 hours was found to be long enough; if left in longer than this the filaments were liable to fragment during the process of washing. For thalloid types 24 hours was not too long. In some cases (*Rhodomela*, *Furcellaria*) the experiment was made of placing the fronds in chloroform water for two minutes, directly on gathering, so as to prevent the nuclei passing into a resting stage before the gradual penetration of the fixative; the results, however, did not compensate for the extra labour involved.

After fixing, the algæ were passed gradually into fresh water and then washed for 24 hours in running water. In cases where it was necessary to preserve the material for future examination, the best medium proved to be equal proportions of 50 per cent. alcohol and 50 per cent. glycerine, as in this the minimum of shrinkage took place, while it was possible at the same time to obtain a very clear and distinct nuclear differentiation with hæmatoxylin. In most cases an endeavour was made to embed direct in paraffin wax, dehydration being carried out on the glycerine embedding system (Dowson, 1922). Microtomed sections were cut from 3–5 $\mu$ in thickness and stained for 24 hours in Haidenhain's Iron-alum Hæmatoxylin. Such sections, it was found, offered the only means of examining minute nuclear details with accuracy, but all delicate structures, such as gelatinous walls and empty antheridial sheaths, were so contracted by the embedding process that it was impossible to distinguish them with any certainty. As a consequence of this effect, the drawings of spermatia made from microtomed sections and published in descriptive articles have given a false impression of the structure of the antheridial group, since the cells are depicted without the delicate surrounding walls (cp. Kylin, 1922, fig. 77 C). Experience shows that these walls are best seen in very thin, stained, hand sections, or, in some filamentous forms (i. e. *Polysiphonia*, *Callithamnion*), in portions of the filament mounted whole. In this case, if the material has been carefully handled, no shrinkage should have occurred. It would seem, therefore, that no complete, or even adequate, idea of the structure of antheridia can be obtained without observations made on both hand and microtomed sections.

## IV. Investigation of the Antheridia and Spermatia in particular Species.

The species described here are arranged on the classificatory system for the Rhodophyceæ, given by Schmitz and Hauptfleisch in Engler and Prantl's 'Pflanzenfamilien' (1897). It will be seen that this does not in any way imply that a similarity in antheridial structure will necessarily be found between two species placed close to one another; the scheme is merely adopted for convenience. In the descriptions an attempt has been made in each case to refer to all previous records of antheridial occurrence, though these accounts are mainly confined to notes concerning the position of the structures on the thallus. As far as possible the species chosen have been those of which there exists no previous detailed description.

### (1) CHONDRUS CRISPUS * Stackh.

Material was gathered at Freshwater and Whitecliff Bay, Isle of Wight, in April 1923, and Wembury Bay (Plymouth) in April 1924.

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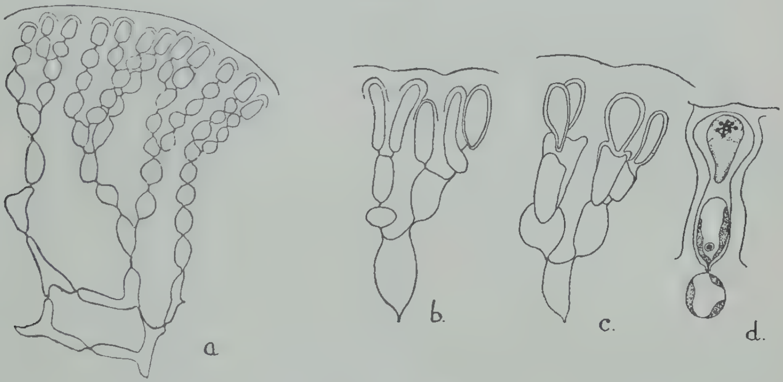
* Antheridia have previously been recorded in a short note by Buffham (1896, p. 183, figs. 2 and 3) and by Darbishire (1902); this condensed account is referred to in the text.

The antheridia develop in this species on the upper parts of the thallus of an otherwise normal vegetative plant. They are recognizable as whitish-pink patches or sori, the youngest regions of which are to be found just below the apex, extending downwards for 3 to 4 mm. Occasionally the sori do not completely cover this area, but are represented by spots or irregular patches; in any case, as Buffham noted, they can best be seen in half-dried material, or even in fronds which have been completely pressed. All the material examined by me has been fully fertile in the spring, but, on the other hand, the plants described by Buffham (from Hastings) and Darbishire were mature in September or October. It seems hardly likely that thalli which were already discharging their spermatia in large numbers in April should continue to do so throughout the summer until the autumn: the more reasonable probability is that there are two seasons of spermatial production on this species, male plants being developed in spring and autumn.

FIG. 1.*



*Chondrus crispus.*

*a.* Section of a vegetative thallus, showing "cortical" structure. × 800.
*b.* Section showing the development of antheridial mother-cells. × 1200.
*c.* Section through similar region, with antheridia arising from mother-cells. × 1200.
*d.* Escaping spermatium, with nucleus in prophase. × 1800.

In a section of a vegetative region of a thallus it can be seen that the central area is occupied by multi-nucleate cells full of contents; these are circular in cross-section, but are elongated in the direction of the length of the thallus. The latter is bounded by small cells in close-set rows extending perpendicularly to the periphery; these chains of rounded cells arise in pairs from the outer cells of the central thallus tissue, and each row is terminated by a single rather elongated cell (fig. 1 *a*). In the upper and youngest parts of the thallus the "cortex" is composed of only a few rows of cells; lower down eight or even more rows may be formed by division, each cell being uninucleate and pigmented and the whole enclosed by a gelatinous "cuticle."

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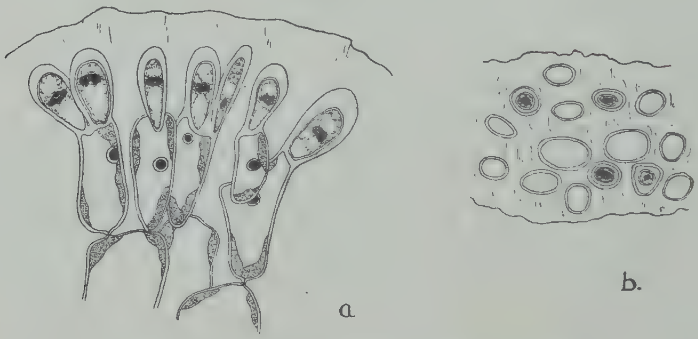
* The drawings throughout were made with the aid of a camera lucida or by projection.

It is the elongated cells forming the outer layer which give rise to the antheridial mother-cells, and this by means apparently of a longitudinal division, for in the soral area of a male frond the last globose cell of each cortical row is always terminated by two narrow elongated cells (fig. 1 *b*). That these are the mother-cells is clearly seen in a slightly older region, for antheridia spring from them (fig. 1 *c*).

At the time of the formation of antheridia the "cuticle" appears to thicken in the soral area; the first antheridia arise laterally from the surface of each of the pairs of mother-cells as thin narrow bodies composed of an upward protoplastic extension surrounded by the mother-cell wall (fig. 2 *a*). The cytoplasmic contents, which enclose a single nucleus but no plastids, are abstricted at a point level with the surface of the mother-cell by the ring-like ingrowth of the surrounding wall; when completed, this curves upward in the centre and is comparable in shape to an inverted watch-glass. The antheridium ripens, becoming more rounded in form, the wall swelling considerably. When nearly mature the cytoplasmic body within can be seen to be entirely surrounded by a clear narrow area which is more refractive than the antheridial wall and may represent the wall of the spermatium (fig. 2 *a*); when the latter escapes I have no doubt that this wall is present as an exceedingly delicate membrane. The antheridium lengthens upwards, the wall piercing the "cuticle," though never apparently protruding beyond it; this "elongated gelatinous body" Buffham measured and found to be "20 μ high and 7 μ thick." A longitudinal split then occurs in the swollen antheridial wall, and the whole contents escape into the surrounding water as a rounded cytoplasmic body containing a single nucleus and clothed in a thin wall. A surface view of the "cuticle" at this time shows it to be pierced by numerous round holes, some of which, as seen from above, appear to be empty, while others show a spermatium nearly

Fig. 2.



Antheridial sorus in *Chondrus crispus*. × 1800.

*a.* Transverse section showing mother-cells arising from "cortical" cells and each subtending two antheridia.

*b.* Surface view of the "cuticle," showing the openings through which the spermatia escape.

extruded (fig. 2 *b*) : if a frond is suspected of bearing antheridial sori, their presence can easily be confirmed by examining the "cuticle" in surface view under the microscope, perforations being visible if the sorus is present.

Darbishire states that only one spermatium arises from each mother-cell, but a second lateral antheridium is clearly developed by the side of the first at the apex of the mother-cell (fig. 2 *a*) ; this grows up, ripens and liberates its contents in exactly the same way as the first one. A third primary antheridium does not seem to be formed, though in such closely-packed tissue where the mother-cells overlie one another it is difficult to make out the number of antheridia connected with each mother-cell. Secondary antheridia are certainly found growing up within the empty walls of the primary ones, but I have not as in some cases (fig. 30 *b* & *c*) been able to identify a third set within the walls of the secondary ones. Each set of spermatia takes a considerable time to travel to the surface of the thick "cuticle," and as a result the second spermatium is often forcing its way up before the first is liberated. A low-power view of a cross-section at this time shows what appear to be loose spermatia scattered at many levels in the "cuticle," the antheridial walls being exceedingly difficult to see. After the formation of antheridia has ceased the thallus probably returns to the normal vegetative structure.

It has already been noted that the antheridial mother-cells are uninucleate and pigmented, the plastids lying mainly at the base and sides of the cell. On the formation of an antheridium the mother-cell nucleus passes upwards and divides mitotically at the base of the protoplasmic projection, one daughter nucleus passing into the latter. The behaviour of this nucleus seems to follow in every detail the stages described for *Furcellaria* (p. 239), and in the ripe spermatium it can be seen to be in early prophase, a number of chromatin granules or "Körnchen" being present (fig. 1 *d*). Apparently no plastids pass from the mother-cell into the spermatium; the structure figured by Darbishire (pl. 6. fig. 32) as "a fragment of plastid" is without doubt the nucleus which he overlooked. When the spermatium is ripe and about to be liberated it measures from 7·5 to 10 $\mu$ in length, being 4 to 5 $\mu$ in diameter * ; it is then a cytoplasmic body clothed in a delicate wall and containing a central or apical nucleus about 4 $\mu$ in diameter suspended above a large vacuole.

### (2) LOMENTARIA OVALIS Endl. = *Chylocladia ovalis* Hook.

While cystocarpic and tetrasporic plants of this species are well known, the antheridial ones have rarely been found, their presence being noted only by Buffham (1896). In spite of continuous search in various localities, the writer has found only a single plant at Swanage, in August 1924.

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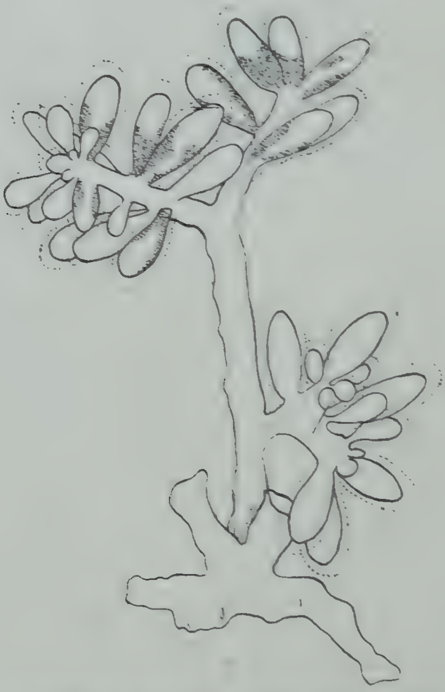
* The measurements of the spermatia and nuclei were made throughout on unshrunken material, except when otherwise stated.

Antheridia are developed in sori upon the obtuse, hollow, bladder-like lateral ramuli in the upper regions (fig. 3). These short branches are borne in dense clusters at the tips of the branching "stem"; the sori arise at their base, spreading up towards the centre, so that the youngest antheridia are to be found about half-way up the hollow sacs, the apex being sterile. The sori are very irregular in shape, sometimes occurring as small isolated patches or elongated lines, or often as one homogeneous mass formed by the fusion of smaller sori. The presence of the groups of antheridia gives a colourless appearance to the portions of the thallus where they occur, and it is by means of these whitish patches, not more than 1 mm. in length, that the antheridial plant can be recognized in the field (fig. 3).

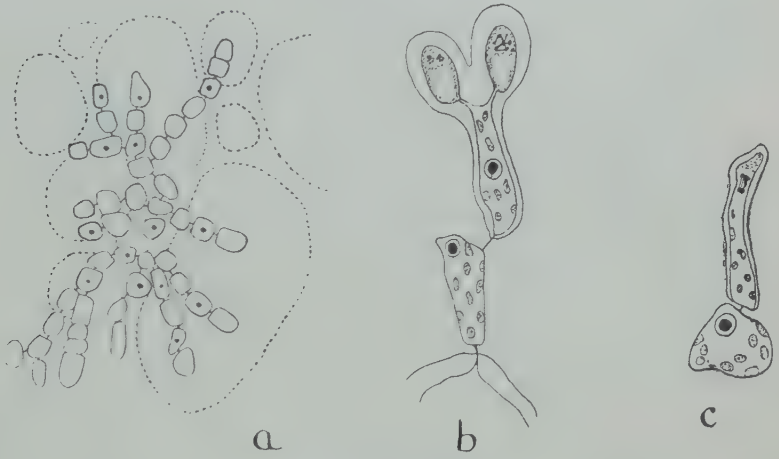
Fig. 3.



Portion of a male plant of *Lomentaria ovalis*. The position of the sori is shown by stippling. The dotted lines around the lateral branches represent the surrounding fringe of unicellular hairs. × 2.

The sterile swollen ramuli are composed of an outer single layer of cells varying in size, while the whole central region is hollow and not traversed by diaphragms; in the youngest branches this central part is filled with a thin watery fluid. It has been shown by many workers that the origin of this structure is from branching filaments of cells which gradually separate from one another, forming a lining layer of cells and leaving a cavity within (*i. e.* Giard, Killian, Schmitz). The whole is clothed with a very thick gelatinous "cuticle." The cells forming the outer layer are irregular in size, and from without the surface appears to be studded with large round cells, each of which is surrounded by a ring of smaller ones filling the interstices; these are all pigmented, multinucleate, and filled with dense contents resembling "Floridean starch." From these cells, both large and small, arise very long unicellular hairs (fig. 4 *a*), which, when mature, are cut off from the thallus by a cross-wall at the base, and themselves possess a thick wall with little cavity except at the apex, where there is a swollen thin-walled knob containing the nucleus and rich protoplasmic contents. These hairs are just visible with the naked eye, and cover the thallus even in the antheridial region (fig. 5 *a*).

Fig. 4.



*Lomentaria ovalis.*

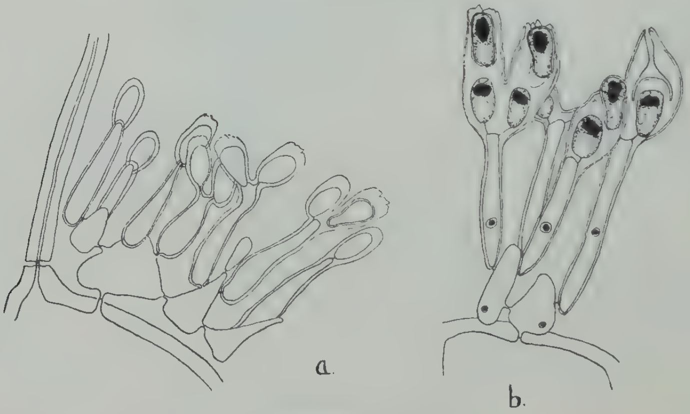
*a.* Portion of young antheridial sorus. The basal cells are seen before the development of the antheridial mother-cells. Vegetative thallus cells indicated by dotted lines. × 800.

*b.* Microtomed section showing single antheridial mother-cell borne on a basal cell and giving rise to two antheridia. The nucleus of the antheridium on the left shows the chromatin separated into two granular masses. × 1800.

*c.* Antheridial mother-cell giving rise to first young antheridium. × 1800.

Unfortunately in the available material the sori were all mature, and it was not possible actually to observe the stages in the formation of the mother-cells. But as far as could be made out, a curious development precedes the production of antheridia, in that a system of branching threads arises from the thallus cells, spreading in every direction over the surface (fig. 4 *a*). When first observed in any isolated region, the threads resemble some well-developed epiphytic growth, but on comparing them over a large area, it is seen that the system is made up of numbers of small groups of cell-threads. Each group has arisen from a central cell which has been cut off from one of the peripheral thallus cells (fig. 5 *a*). The order of development is therefore somewhat similar to that found in *Callithamnion brachiatum* (fig. 30 *a*) or *Griffithsia corallina* (fig. 22); a central cell cut off from a thallus cell gives rise by division to a system of branching threads which spread over the surface of the thallus and are composed of small uninucleate pigmented cells linked to one another by protoplasmic connections (fig. 4 *a*). From each cell of these filaments two or three antheridial mother-cells grow out as small projections, generally densely pigmented and containing one nucleus; the cells of the filaments therefore function as basal cells. The mother-cells increase greatly in length, stretching upwards until long and narrow and measuring about 15–20 $\mu$ in length (fig. 5 *a* & *b*). Their apex is somewhat square and blunt, and laterally from this primary antheridia are formed; these arise as small protoplasmic protuberances, clothed in the mother-cell wall, and containing a single nucleus derived from the division of the mother-cell nucleus. Two primary antheridia are always developed and sometimes three (fig. 5 *b*); there does not appear to be any general regularity in the number as in other species, and though not developing quite simultaneously, there is not such a marked interval between their production as is often the case. They swell and increase in size and are

FIG. 5.



*Lomentaria ovalis.*

*a.* Outline drawing of a section through an antheridial sorus, showing central cell giving rise to lateral ones. From each of these, two or three antheridial mother-cells arise, each bearing ultimately two or three antheridia. A unicellular hair is seen (left). × 1800.

*b.* Section of an antheridial sorus, showing the production of secondary antheridia. Left—first spermatia have not yet escaped. Right—empty sheath of primary antheridium, with a secondary one growing up within. Plastids omitted. × 1800.

abstricted from the mother-cell by the ingrowth of the gelatinous wall of the latter, always, however, remaining connected by a very fine protoplasmic strand (fig. 5 *b*) and when ripe measuring 4–5 $\mu$. At this stage there is a most striking resemblance in form between the mother-cell bearing the antheridia and a basidium with two sterigmata bearing basidiospores. The walls of the antheridia which appear as surrounding gelatinous sheaths are very difficult to see, but it is clear that they are much stretched upwards, piercing the "cuticle" and becoming split and frayed at the apex (fig. 5 *a*). Finally a decided split occurs, cleaving the whole wall, and through this the spermatium escapes, being by now clothed in a delicate membrane; the antheridial wall, released from the pressure of the spermatium, at once contracts, only leaving a narrow cavity (fig. 5 *b*). Meanwhile a secondary antheridium develops within the sheath of the primary one (fig. 6 *b*, right). This sometimes occurs before the release of the first, but in any case the development and liberation are exactly similar in the case of both primary and secondary spermatia. No tertiary antheridia appear to be formed. A mother-cell may therefore produce six antheridia altogether, three primary and three secondary.

The mother-cell of the antheridia is both uninucleate and strongly pigmented, containing granular contents. In the resting condition, the nucleus, which consists of a deeply-staining central region and a colourless outer area is central in position (fig. 4 *b*). On the formation of antheridia it moves to the apex of the cell, where a small projection is arising, and there divides mitotically, the spindle being arranged parallel to the long axis of the mother-cell, the whole figure measuring not more than 2 $\mu$. The chromatin is visible at metaphase as a darkly-staining band across the equator of the spindle and at anaphase as two minute dark dots, one at either pole (fig. 4 *c*). One of these daughter nuclei passes into the young antheridium in a resting condition. There it enters shortly into early prophase, the chromatin being distributed as irregular dark thickenings along the threads. Finally, at the time of liberation the chromatin is concentrated in regular dark granules connected by delicate threads and often gathered into two groups within the nucleus, which is now apical in position (fig. 4 *b*); the antheridial nuclei are, like the spermatia, very small and measure only about 2 $\mu$ in diameter. The spermatium is unpigmented but contains a considerable amount of granular cytoplasm arranged around a large vacuole beneath the nucleus.

### (3) CHAMPIA PARVULA * (J. Ag.) Harv. = *Chylocladia parvula* Hook.

Material consisted of one plant gathered at Perros, Brittany, July 1924.

The antheridial plants of *Champia parvula* are exactly similar in outward

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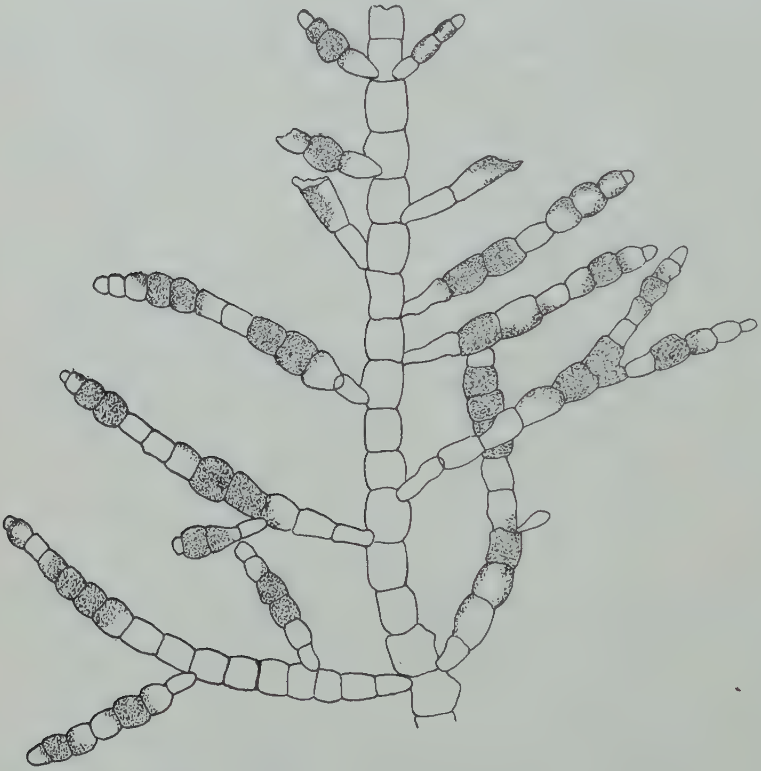
* The presence of antheridia in this species has previously been noted by Davis (1896, p. 111) and Nott (1896).

appearance to the vegetative ones, but they may be distinguished on close examination by pale patches scattered over the ramuli. These colourless areas are the sori which, according to Davis, may appear as "caps at the end of the stem, but more often as bands around the older parts of the frond." In the one plant collected it is the exception to find sori at the tips of branches, but they usually occur on two or more segments of the thallus (fig. 6). These segments are more swollen and rounded than the vegetative ones, and the colourless cells may either cover them completely or may be scattered in small patches on their surface.

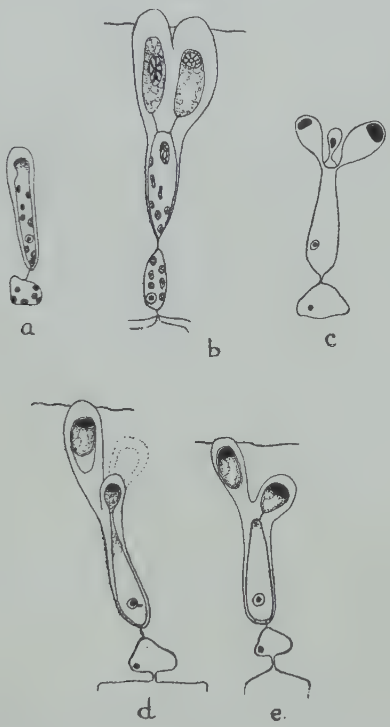
FIG. 6.



Part of an antheridial plant of *Champia parvula*. Sori represented by stippling. × 8.

The development of the antheridial mother-cells in *Champia parvula* is from a system of branching threads. Nott pointed out that the basal cells of these threads arose and were cut off from the angles of the peripheral cells of the thallus, and by branching they formed "rows of cells which radiate out in every direction from the stalk cells." This, it will be seen, is an entirely similar development to that found in *Lomentaria ovalis*, the cells being in the same way uninucleate, pigmented, and filled with dense contents. From these basal cells, antheridial mother-cells are cut off singly or in pairs, and these, when fully developed, attain to as much as 10 or 11 $\mu$ in length (fig. 7); they are slightly pigmented, and the nucleus is often difficult to make out owing to the presence of granular contents. From these cells the antheridia develop, first as slight blunt projections (fig. 7 *a*) and later, when containing a single nucleus, becoming stretched and abstricted at the base (fig. 7 *d*); they remain, however, in protoplasmic connection until fully ripe, when the connection is broken and the spermatium escapes. The antheridial wall when mature pierces the "cuticle" to a sufficient extent to permit the escape of the spermatium through an apical split direct into the surrounding medium (fig. 7 *b*). As a general rule three antheridia appear to be developed from each mother-cell, standing around the slightly flattened apex at three different growth-stages (fig. 7 *c*). These three can never be seen at the same focus, but at a high focus it is

FIG. 7.



Development of antheridia in *Champia parvula*. × 1800.

*a*. First signs of development of antheridium from mother-cell.
*b*. Microtomed section showing the nuclei in different stages of prophase in the ripening antheridia.
*c*. Reconstruction of a mother-cell bearing three antheridia.
*d*. Antheridial mother-cell seen at a high focus.
*e*. Same at a low focus, showing the third antheridium.

generally possible to see one or two, and a third becomes visible at a low focus (fig. 7 *d* & *e*). Secondary antheridia are also developed in this species on the liberation of the primary ones, but there is no sign of tertiary ones. Each mother-cell has, therefore, the possibility of developing six antheridia.

The cytological changes in the production of this structure are entirely similar to those in *Lomentaria ovalis*. The mother-cell nucleus moves to the apex of each mother-cell after a young projection has arisen and there divides, one nucleus passing into each antheridium in a resting state. While this nucleus is moving to the apex of the latter it passes into an early prophase (fig. 7 *b*, left) until, when the spermatium is mature, a number of deeply-staining granules are present, united by delicate threads (fig. 7 *b*, right). The nucleus is in this condition when the spermatium is liberated.

The resemblance between the method of development of the antheridia in *Champia parvula* and *Lomentaria ovalis* is so great that, given a transverse section of a sorus, it would be almost impossible to state from which species it had been cut. In both, the development proceeds in the following stages :—

1. Central cells are cut off from the peripheral cells of the thallus.
2. These central cells by division gave rise to branching rows of basal cells extending over the surface of the thallus.
3. From each of these arise two or three elongated mother-cells.
4. These give rise sub-terminally to two or three antheridia.
5. These on attaining maturity liberate their spermatia through an apical split in the antheridial wall.
6. Secondary antheridia are developed within the empty sheaths of the primary.

Such striking similarity in the details of antheridial production cannot fail to emphasize the close systematic relationship between the two genera.

### (4) NITOPHYLLUM HILLIÆ * Grev.

Material consisted of many fertile thalli dredged in Plymouth Bay in April 1924. The alga was found at the same time attached to the rocks in the tidal region, but in this position was always sterile.

The antheridia occur on separate plants and apparently never in combination with the tetraspores or cystocarps. The male plants are normal in size and general appearance, but are easily distinguished when fresh by the presence of numerous little pale spots or patches, exactly similar in position to the darker areas formed on the tetrasporic plants. These are the disconnected sori, and are most marked near the base of the thallus, beginning roughly about 5 mm. from the point of attachment and decreasing in size towards the irregular margin, where the youngest sori are to be found as minute pale spots. The sori occur on both surfaces, the largest ones near the base becoming more or less confluent with one another, forming irregular streaks running in vaguely parallel lines between the veins, but never crossing the latter.

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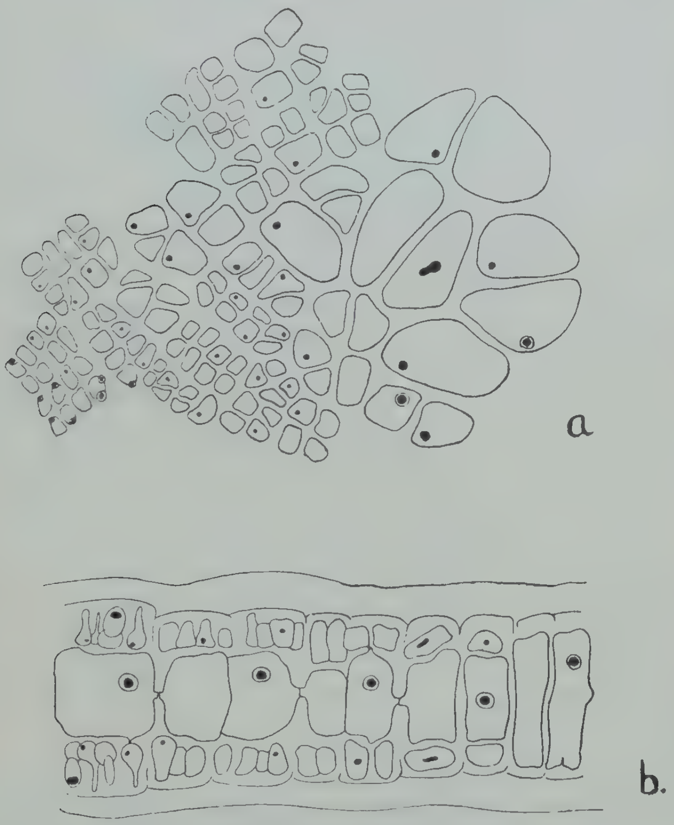
* The presence of antheridia in this species has previously been noted by Thuret (1855).

The normal antheridial thallus before developing the reproductive bodies consists of a single layer of cells, except in the region of the veins, where it becomes three cells in thickness; antheridia are, however, always borne in the single-celled region, the cells composing the tissue of the frond here being three to four times as long as broad and containing numerous small plastids clustered at either end, as well as a single nucleus generally central in position; the whole is enclosed in a gelatinous "cuticle" (fig. 8 *b*). On the formation of antheridia the single cells cut off one small cell at each end, by walls parallel to the surface of the frond. Each small cell appears rectangular in

Fig. 8.



Development of antheridia in *Nitophyllum Hilliæ*. × 600.

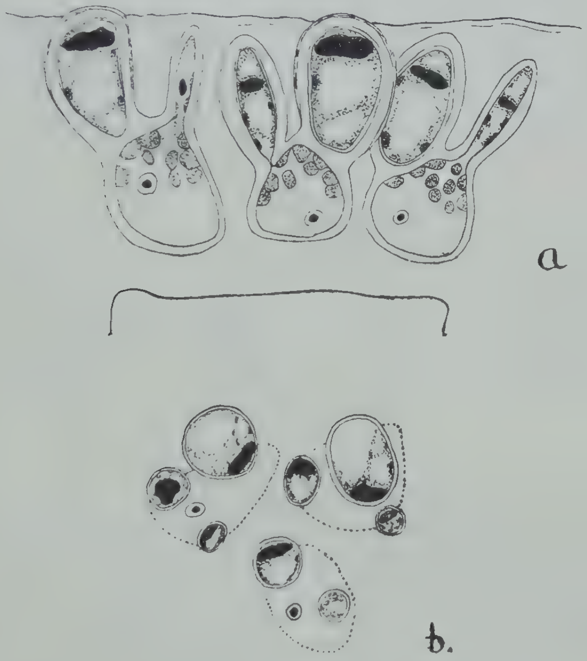
*a.* Surface view of edge of young sorus, showing gradual division of cells to give antheridial mother-cells.

*b.* Transverse section through a similar position.

surface view, is uninucleate and pigmented (fig. 8 *b*); the thallus is now three-layered in the soral regions between the veins. Each of these small cells divides by a vertical wall and then by a second wall, also vertical, at right angles to the first, thus giving rise to a little group of four uninucleate cells in a single layer (fig. 8 *a*). Each of these is then divided by two additional intersecting vertical walls giving finally sixteen cells in a single layer grouped together as if in a little packet (fig. 8 *a*). In the soral areas, therefore, the original thallus cells are clothed on either surface with groups of sixteen small pigmented uninucleate cells, the whole covered with the gelatinous "cuticle" (fig. 8 *a*); these cells, which are now somewhat three-cornered in surface view, are the antheridial mother-cells and from them the antheridia arise. It will be seen that this development is in many respects similar to that described for *Martensia* (Svedelius, 1908) and also for certain species of *Delesseria* (Kylin, 1922); in the former case the thallus also becomes three-layered on the formation of antheridia, the middle layer playing no further part in the development and the outer layers dividing up to give numerous small cells, 30 to 50 being formed from each original surface cell. These antheridial mother-cells are uninucleate in *Martensia* as well as in *Nitophyllum*, but in the former the original vegetative cell contains many nuclei, and these gradually diminish in number as continual divisions take place. In both *Delesseria sanguinea*, *D. alata*, and *D. sinuosa* a somewhat similar type of development occurs (Kylin, 1922). Here the male thalli, before the formation of antheridia, are one-layered, except in the region of the midrib or of smaller veins where there may be as many as seven rows of cells; in each case an outer layer of cells or "Rindenschicht" is formed by the cutting-off of small cells on each surface. The cells then divide by perpendicular walls, giving a larger number in a single layer, no intercalary divisions taking place; how many cells are formed from each surface cell is not stated. In these three species of *Delesseria* no particulars of the number and arrangement of the nuclei in these divisions are given, though the large vegetative cells are known to be multinucleate; in each case, however, the antheridial mother-cell contains only a single nucleus.

In *Nitophyllum Hilliæ* the antheridia first arise from the mother-cells as very narrow beak-like processes enclosed in a comparatively thin wall which is merely an extension of the mother-cell wall forced up through the thick "cuticle" (fig. 9 *a*). This single sub-terminal antheridium is very small and thin compared with those formed in other genera as *Griffithsia*, where there is no compression such as arises here from the close packing of the mother-cells side by side. Soon, however, the dense protoplasmic contents are abstricted from the mother-cell by the gradual ingrowth of the surrounding gelatinous wall (fig. 10 *a*), though remaining for some time in connection (fig. 9 *a*). The spermatium grows and swells, becoming much enlarged and almost spherical; the single nucleus occupies a curved apical position, beneath which is a large vacuole crossed here and there by strands of cytoplasm (fig. 9 *a*). The antheridial wall is now stretched to such an extent that it is actually forced beyond the "cuticle," and shows at this stage a distinct narrow outer layer, a swollen middle one, and a delicate inner refractive region around the spermatium (fig. 9 *a*). The latter finally escapes directly into the water around, through an apical split in the antheridium wall (fig. 10 *a*). But before this occurs a second antheridium arises at another corner of the triangular mother-cell and begins to develop, and even a third antheridium is commonly formed before the first spermatium has passed out. On looking down, therefore, on an antheridial sorus from above, one sees little groups of antheridia in threes, each member of the trio being at a slightly different stage of development, while far below (as it seems) can be seen the surface of the pigmented mother-cell (fig. 9 *b*). Each of these rounded spermatia is liberated in turn through the apical split in the antheridial wall. The pressure exerted upon this wall by the spermatium during its difficult outward passage must be considerable,

FIG. 9.



*Nitophyllum Hilliæ.* × 1800.

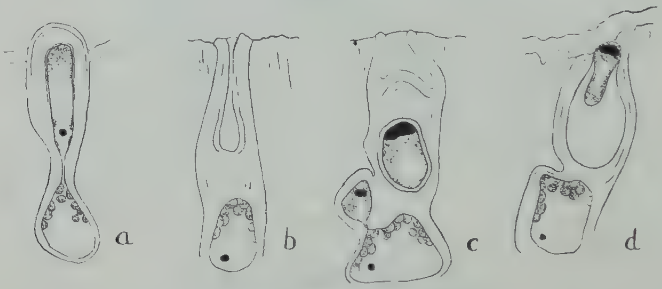
*a.* Transverse section of a young antheridial sorus, showing the thin "cuticle" pierced by the antheridia in different stages of development.

*b.* Surface view of a similar sorus, with group of three antheridia developing successively from mother-cells.

for immediately after its liberation the surrounding wall contracts. Though the wall is supported by the "cuticle" and cannot shrink back upon the mother-cell, yet the contraction is such that only a narrow slit-like opening remains, and even that is often difficult to find (fig. 10 *b*). In sori near the base of the frond, where the "cuticle" is thicker and where the spermatium must traverse a greater distance before liberation, antheridia have several times been found with shrivelled spermatia caught in their openings (fig. 10 *d*); evidently here the force which causes the expulsion of the spermatium was not quite sufficient to overcome the resistance of the wall. It is noticeable that in these lower sori the spermatia are longer, thinner, and smaller than in the upper ones where the "cuticle" is not so thick.

As a general rule, secondary antheridia appear to be formed within the walls of the primary ones, developing in the same way (fig. 10 *c*). In the lower regions of the thallus, however, they could not always be found, and apparently do not occur here regularly.

FIG. 10.



*Nitophyllum Hilliæ.* × 1800.

Antheridia from old sorus at base of a frond (optical section).

*a.* Young antheridium in process of gradual abstriction.
*b.* Empty antheridium after escape of first spermatium.
*c.* Secondary antheridium forming within the empty wall of the primary one.
*d.* Shrivelled spermatium, apparently unable to escape from an antheridium.

### (5) NITOPHYLLUM LACERATUM* Grev.

Material was obtained from dredgings in Plymouth Bay, April 1924.

The antheridia in *Nitophyllum laceratum* are borne on leaflets which may be anything from 1 to 20 mm. in length. These are found in spring at the apex of the old and ragged growth of the past year, as many as ten or twelve growing on the divided tip of one old thallus. They show branching veins, and the antheridia develop as lateral pale pink patches, the sori gradually extending round the apex, leaving a non-fertile margin and central region. The male plants are apparently not common, for out of a large number of specimens brought in by dredging at Plymouth, the majority of which were either tetrasporic or cystocarpic, antheridia were found on less than a dozen.

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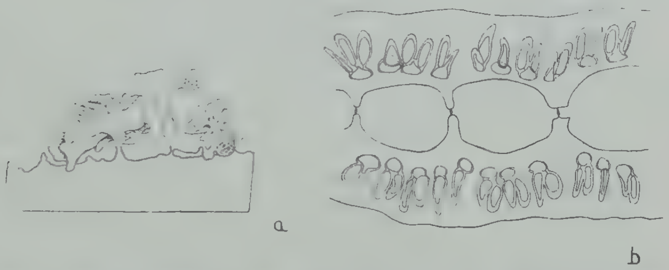
* There are no previous references to antheridia in this species.

The development of the antheridia resembles closely that described for *Nitophyllum Hilliæ*. The leaflets are composed of a single layer of elongated cells containing generally several nuclei and plastids clustered at the two outer surfaces.

When about to become fertile, surface cells are cut off above and below, making the thallus three-layered. Each of these divides, as in *N. Hilliæ*, to give, in many instances, sixteen smaller cells. In some cases the full number of divisions does not seem to be attained, and only twelve or thirteen cells are formed from an original surface cell ; this, however, does not seem in any way to prevent such cells from fulfilling their functions as normal mother-cells. The antheridia are formed in exactly the same way as in *N. Hilliæ*, and there is therefore no need to repeat the description (see p. 196). They arise from each mother-cell in succession (fig. 12 *b*), being at first exceedingly thin and narrow as in the previous species, and later rounding off and becoming 6 to 8 $\mu$ in length. Secondary antheridia appear regularly to be formed and to pass out through the empty sheaths. The wall surrounding the young spermatium while still enclosed in the antheridium is very clearly seen in this species (fig. 12 *a*).

FIG. 11.

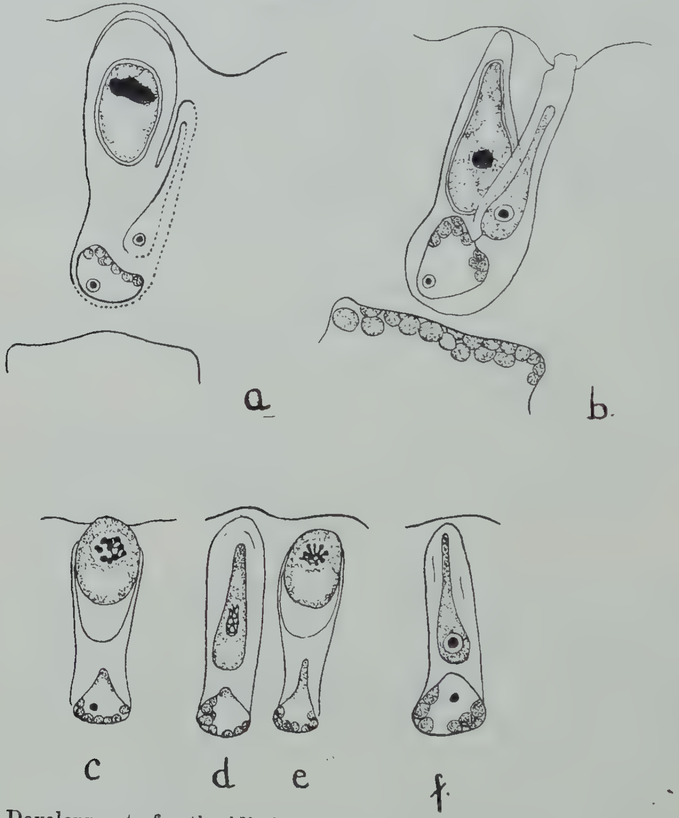


*a*. Portion of a thallus of *Nitophyllum laceratum* bearing laterally rosettes of leaflets known as *Gonimophyllum Buffhami*. These are covered with antheridial sori, and also bear tetraspore-like structures. × 10.

*b*. Section through an antheridial sorus of *N. laceratum*. The central cells are clothed on the outer surfaces with mother-cells bearing antheridia. × 690.

The mother-cell nucleus lies at the base of the pigmented cell and only passes upwards to divide. This division takes place when the antheridium is represented by a very short-pointed process, and it is noticeable that the antheridial nucleus on formation passes at once into a resting stage with a central darkly-staining region and a clear area around (fig. 12 *f*). As the antheridium lengthens, the nucleus moves along it as a narrow body surrounded by dense protoplasm (fig. 12 *d*), until finally, when the spermatium has been cut off, the nucleus is at the apex, suspended by strands of cytoplasm with a vacuole below (fig. 12 *a* & *c*). Before the spermatium has reached maturity this nucleus is seen to be entirely made up of a tangled mass of irregularly thickened threads (fig. 12 *e*). When the spermatium is ripe the chromatin masses on these threads have formed a number of separate granules strung together by means of delicate linin threads (fig. 12 *c*). The nucleus, measuring about 2·5 μ in diameter, is in this state when the spermatium escapes.

FIG. 12.



Development of antheridia in *Nitophyllum laceratum*. × 1800.
Antheridial mother-cell at high (*a*) and low (*b*) focus, showing the three primary antheridia.
*c* to *f*. Successive stages in the development of spermatia.

The similarity between *N. Hilliæ* and *N. laceratum* in the method of formation and structure of their antheridia is so close that it would be impossible to tell the species from a transverse section of a sorus. On the other hand, the two species are easily separated by the position of the male organ, these being situated on the thallus in the first case and on special fronds in the second. In *N. Gmelini*, where the antheridial sori are said to be borne either near the margin of the thallus or on special processes on the margin, one would conclude from Buffham's figure (1893, fig. 21) that the development is in all probability similar. In *Nitophyllum* therefore as in *Delesseria*, so far as is known the development of the antheridia is constant throughout the genus, but the position of the sori may be either on the normal thallus or on special antheridial fronds.

### *Note on* GONIMOPHYLLUM BUFFHAMI Batt.

Batters (1892) described a specimen of *Nitophyllum laceratum* bearing groups of minute leaflets on the surface or at the margin of the thallus. These leaflets, arising from a "basal cushion," were said to be covered indiscriminately with antheridia, procarps, and tetraspores. The whole structure was regarded as a parasitic alga and described under the name of *Gonimophyllum Buffhami* Batt. Specimens of *N. laceratum* were dredged from Plymouth Bay in April 1924, bearing similar small rosettes of crinkled leaflets, and these have been examined for reproductive organs. In each rosette some part or the whole of the surface was covered with colourless sori of antheridia, while in three specimens antheridial and tetraspore-like structures occurred in close proximity, even being found in the same rosette (fig. 11 *a*). From a slight examination it seems probable that the tetraspores do not develop normally in these cases and never come to maturity. The structure of the leaflets and the development of the antheridia appears to be exactly similar in every detail to that described above for *N. laceratum*. This resemblance is so striking, that, combined with the fact that the procarps and cystocarps are also said to resemble those on *N. laceratum* "in all essential particulars," the question arises as to whether the structure is in reality a parasitic alga. The evidence seems to point towards the probability that these curious rosettes of leaflets may be an abnormal outgrowth of the thallus tissue of *N. laceratum*. The cause of this abnormality is at present a matter of speculation, but it does not seem unlikely that the outgrowth may be induced by the presence of some intercellular or intracellular endophyte.

### (6) LAURENCIA PINNATIFIDA* Lam.

Material was obtained from Shanklin, Swanage, and Plymouth, January and May, 1923 and 1924.

Observations show that plants bearing antheridia ripen in the spring on the south coast of England, thus coinciding with the production of the female organs. The male plants are numerous, and there is no difficulty in obtaining specimens, due possibly to the fact that they are as conspicuous as the female and more so than the tetrasporic thalli, and do not therefore give the impression of being in the minority as in many species. The antheridial plants can easily be distinguished by means of their fat swollen pinna tips, due to the presence of embedded conceptacles with dense yellow contents; if in any doubt, a slight examination with a hand-lens will at once reveal the circular openings of these depressions, often with the tips of the antheridial filaments showing within.

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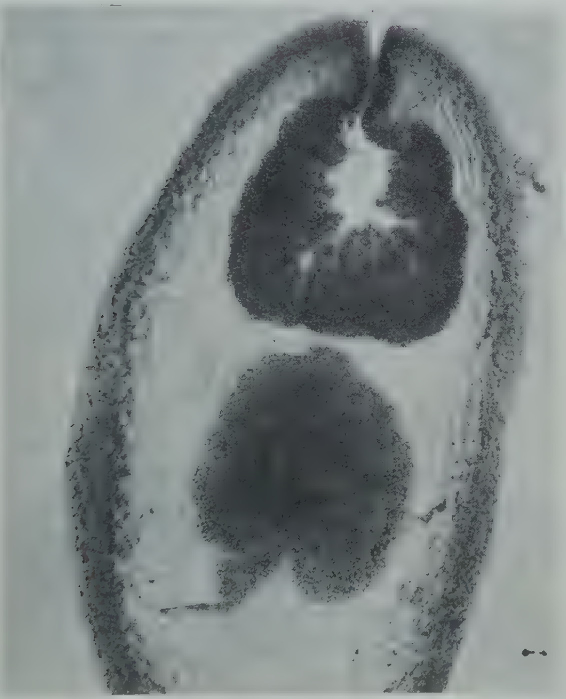
* Short notes recording the presence of antheridia have been made by Greville (1830, p. 110), Derbes and Solier (1850, p. 261), and Thuret (1855, p. 17). Such facts as are known about the details of development are found in Falkenberg's and Kylin's descriptions (1901 and 1922 respectively).

The antheridia are borne on axes lining the conceptacles. From the published figures it appears that the latter vary greatly in shape, some having a wide opening and cup-like form, while others are contracted at the apex, leaving only a narrow entrance to the cavity. Both types of receptacle are figured and described by Harvey (1849, pl. 55. figs. 4, 5) as being either "cup-shaped" or "urn-shaped," the former apparently occurring on dwarf plants with broad, flat ramuli, which are distinguished as var. *littoralis*. Kylin (1922, fig. 81*a*), however, figures only the cup-shaped type, evidently regarding this as typical, since he mentions no other. On the other hand, every male frond of the species examined by the writer has had conceptacles of the urn-shaped form, with a contracted entrance leading to the swollen cavity within (cp fig. 13).

The conceptacles have been shown by Kylin to be formed by rapid growth of groups of cells around the apical cell of a pinna, the latter ceasing to function and becoming carried down into a concave depression. At the same time, there is carried down a group of hairs which develop from the outer layer of cells at the apex of each fertile pinna, and these line densely the whole internal wall and even the ostiole of the conceptacle (fig. 13), though fig. 81*a* in Kylin's paper gives the impression that they only occur along the floor of the latter. Those in the uppermost region remain sterile, guarding the entrance, while the remainder form the axes around which the antheridial mother-cells and the antheridia are borne. These axes originally consist of a single row of cells, but later they often become by division two or more rows thick at the base, and are terminated by two or three "giant" cells; it is possible that these latter may be concerned in the extrusion of the spermatia from the receptacle. Lewis (1909, p. 656) suggested that in *Griffithsia Bornetiana* the spermatia are only liberated from the antheridia when pressure is exerted on the cells of the thallus; his idea might be extended to *Laurencia*, for when slight pressure is applied to the receptacles, masses of spermatia contained in a drop of mucilage are exuded through the ostiole. Probably this mucilaginous drop is obtained from the giant cells at the tip of each antheridial filament, for in older receptacles, where the majority of spermatia have escaped, these cells are found collapsed and empty of their mucilaginous yellow contents.

When fertile, according to Kylin, each cell of the upstanding axes cuts off four pericentral cells, and these divide again several times so that the whole axis is densely clothed with a number of pericentral cells (1922, fig. 81 *b*, *c*). Each of these becomes an antheridial mother-cell and gives rise to a number of antheridia. The mother-cells are pigmented and flattened in shape, with broad bases which lie along the axes ; each one is said to abstrict three to four antheridia. Observations show, however, that the usual number of primary antheridia produced from a mother-cell is four, formed in regular succession, no two being ever found in the same stage of development on one mother-cell (fig. 14 *a* & *b*). When ripe each is a large, clumsy-looking colourless body with a single apical nucleus, a central vacuole, and a little peripheral protoplasm (fig. 14 *d*) ; the surrounding wall swells considerably, especially at the apex, and the contents are liberated as a single spermatium through a wide split at the top (fig. 14 *b*). While still within the antheridium, the spermatium has the appearance of being surrounded by a clear transparent area which might either be a wall or an empty space (fig. 14 *a*) ; when extruded the body is distinctly seen to be enclosed in a delicate gelatinous

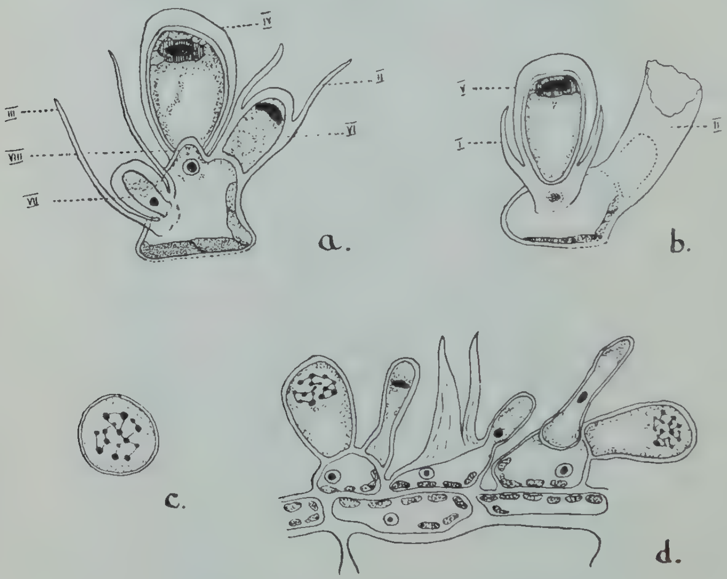
FIG. 13.



Photomicrograph of a longitudinal section through an antheridial conceptacle of *Laurencia pinnatifida*. × 90.

wall (fig. 14$c$). The antheridial sheath which remains behind is often split down to the base by the difficult exit of the fat spermatium (fig. 14$d$), which, when liberated, measures 7 to 10$\mu$ in diameter; these sheaths are apparently of a thicker consistency than in most other species, for on staining they can be seen clustered over the axes and are very conspicuous. Kylin makes no mention of the method of escape of the spermatium or of the presence of antheridial walls; this may possibly be accounted for by the fact that, judging from his figures, his work was solely done with the aid of microtomed sections. But so resistant are the walls in this species that it would appear impossible to overlook them even in microtomed sections. Nor does the above-mentioned author give any indication that the first crop of spermatia is followed by a later one, yet this is undoubtedly the case. In an older conceptacle, within each empty antheridial sheath a new antheridium can be seen growing up (fig. 14$a$); this passes through the same stages as a primary one and, finally, in the same way, discharges its spermatium. No signs have been seen of more than two antheridial sheaths, one within another, indicating the production of more than two sets of antheridia; there seems no obvious reason why antheridial production should

Fig. 14.



Development of the antheridia in *Laurencia pinnatifida*. × 1800.

*a* & *b*. Optical sections of an antheridial mother-cell, seen at high and low focus respectively. The antheridia are numbered in order of development.

*c*. Single escaped spermatium showing the nucleus in prophase.

*d*. Microtomed section showing the development of antheridia and the nuclear stages.

not continue through many generations of spermatia as in the Nemalionales (see pp. 242, 245), but in this species, at any rate, this does not seem to be the case.

In addition to the development of antheridia upon the outgrowing axes, antheridial mother-cells are formed in large numbers among the layers of cells lining the cavity of the conceptacle in between the antheridial filaments. These mother-cells with broad bases are cut off from the inner layer of cells, and in exactly the same way develop antheridia in succession. Appearances suggest that every cell lining the cavity is capable of producing mother-cells, and this productive area is naturally much increased by the axes extending into the centre. Also, since the mother-cells are not closely packed in rows, as in *Chondrus* (p. 185), freedom is allowed for the outgrowth of antheridia all around them, large numbers of these bodies being developed by this means in a conceptacle. Since a single average-sized antheridial plant may bear well over 200 conceptacles, it is evident that this species produces a very large number of spermatia. As far as I am aware, there are no records of the presence of the spermatia upon the trichogynes, though Kylin, in his account of the development of the procarps (1922, p. 127), apparently takes it for granted that a fusion of the spermatial with the carpogonial nucleus actually occurs.

The cells lining the conceptacles and those of the antheridial axes are all uninucleate; the mother-cells also contain a single small nucleus, and this divides at the base of each projection, one nucleus passing slowly up the young antheridium, the other returning to the lower end of the mother-cell. When the antheridial nucleus is first cut off, it appears as a small darkly-staining body showing no signs of granulation (fig. 14 *d*); at the time of escape of the spermatium this nucleus has greatly increased in size, and lies at the apex of the antheridium as a slightly oval body about $2 \times 2{\cdot}5\,\mu$ in diameter; it is then composed of a number of deeply-staining chromatin granules or "Körnchen" connected together by delicate threads (fig. 14 *d*). Kylin states that there are about twenty of these granules present in each nucleus, and with this estimate I should agree, though, owing to the thickness of the nuclei, it is difficult in most cases to make out more than 15 or 16. On escape of the spermatium the cytoplasmic contents become rounded off around the nucleus, the vacuole disappears, the nucleus occupying almost the whole of the spermatium with the exception of the small peripheral cytoplasmic layer within the delicate wall (fig. 14 *e*). The changes in structure from the moment when the nucleus is cut off to the liberation of the spermatium were not all so clearly observed as in *Furcellaria* (p. 237); it can, however, be seen that the nucleus first appears as a small homogeneous body, later showing the well-known granules. This affords support to the view that, when first formed, the nucleus returns to the normal resting stage, only to pass immediately into the earlier stages of a further division.

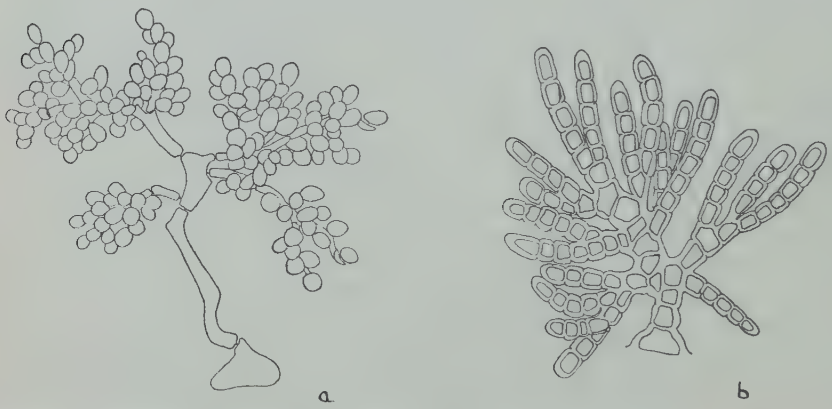
(7) LAURENCIA OBTUSA* (Huds.) Lam.

Material consisted of one plant gathered at Primel, Brittany, in July 1924.

The antheridia in *Laurencia obtusa* have, since the days of Kützing, been known to occur in shallow open cups, at or near the tips of the pinnæ. These cups are densely crowded together, giving to the plant a tufted bushy appearance; on examination with a lens many of them seem to be sterile, but in others colourless clusters of ripe antheridia can be seen at the wide entrance to the conceptacles, and following the slightest pressure on the latter these clusters are at once extruded as gelatinous masses.

The conceptacles appear to be formed in a similar manner to those in *Laurencia pinnatifida*, though their ultimate form is somewhat different, being shallower, with a wide mouth, at the entrance to which hardly any contraction has taken place. The inner walls are lined with richly-branched hairs, some of which remain sterile permanently, while others give rise to the antheridial mother-cells and antheridia; about eight to twelve axes showing this latter development are present in the ripe conceptacle. The sterile hairs, which are apparently absent in the lower part of the conceptacle of *L. pinnatifida*, show a very bushy appearance (fig. 15 *b*); they do not grow to the same length as the fertile ones, but remain in contact with the wall of the receptacle, forming a close "undergrowth." The fertile hairs are made up of branching rows of long narrow cells, poor both in pigment and in protoplasmic contents (fig. 16 *a*). On these cells the antheridial mother-cells

FIG. 15.



Branched axes dissected out from an antheridial conceptacle of *Laurencia obtusa*. × 600.

*a*. Fertile axis bearing numerous antheridia.

*b*. Short sterile axis.

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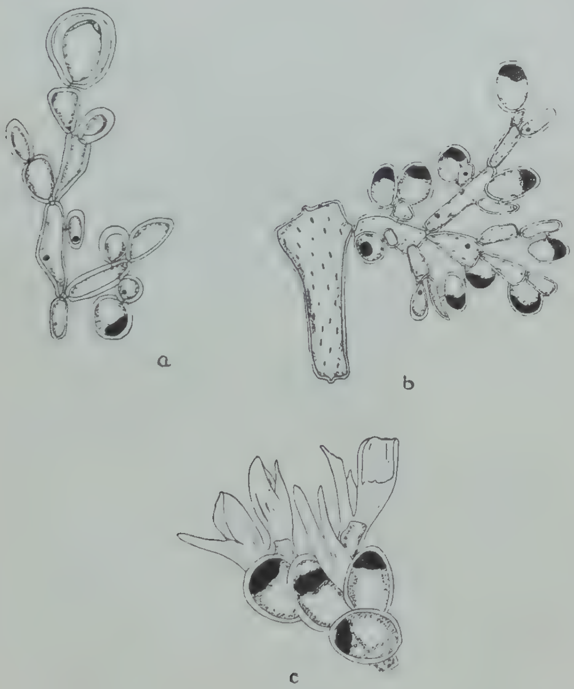
* The presence of antheridia in this species has been recorded by Kützing (1845, pl. 55. fig. *d*), Derbes and Solier (1856, p. 75), Harvey (1849, pl. 148), Buffham (1893, p. 293), and Falkenberg (1901, p. 247).

arise, the earliest formed appearing near the base of the axis ; a progressive development therefore takes place both in the mother-cells and the antheridia, the base of the axis often being fully fertile, while the apex shows no sign of antheridia ; the axis is sometimes terminated by a swollen "giant" cell, but this does not invariably occur (fig. 16*a*). The antheridial mother-cells are cut off as single small pericentral cells around the axial cells, sometimes occurring opposite one another, but often being scattered, or even terminating a branch (fig. 16 *a*) ; in any case they are comparatively small, uninucleate, and poorly pigmented. From each mother-cell two primary antheridia are formed, following one another very closely and appearing almost at the same stage of development (fig. 16 *b*). They arise in the usual way as protoplasmic outgrowths, clothed in the mother-cell wall, by the ingrowth of which they are abstricted. They then swell rapidly, the wall always remaining rather thin, but the spermatium becoming almost spherical and about 6 to 9 $\mu$ in

FIG. 16.



Development of the antheridia in *Laurencia obtusa*.

*a*. Apex of an antheridial filament terminated by a "giant" cell. A single antheridium has developed on a mother-cell (right). × 1200.

*b*. Lower region of the same filament ; the mother-cells bearing ripe antheridia. × 1200.

*c*. Apex of an older filament, showing empty sheaths (above) through which the primary spermatia have escaped. × 1800.

diameter. At this stage a branching filament covered with ripe antheridia is almost visible to the naked eye, and strongly resembles a miniature cluster of grapes (fig. 15 *a*). The gelatinous walls are soon split by the swelling of the spermatium, and the latter escapes, clothed in a delicate membrane and leaving behind it the tough antheridial wall (fig. 16 *c*). Secondary antheridia arise within these sheaths, developing and forcing their way out in a similar manner; it is noticeable that at the time of exit of the first spermatium there is no sign of the second, this appearing later. Anything beyond two antheridial sheaths, one within the other, has not been seen.

As in *Laurencia pinnatifida*, the cells of all the branching axes and the mother-cells are uninucleate. The behaviour of the antheridial nucleus is exactly similar in the two species, there being apparently rather fewer granules ultimately formed in *L. obtusa*. Owing to the fact that the only available material was not well fixed for cytological details, the exact number could not be counted.

It will be seen that the chief difference between the two species lies in the structure of the antheridial axes and the reduced number of antheridia in *L. obtusa*. In the latter, antheridial mother-cells are not formed from the cells which actually line the conceptacles, but only from the cells of the filaments; even all these are not fertile, whereas in *L pinnatifida* there are normally no sterile axes except around the ostiole. Again, four antheridia develop from each mother-cell in *L. pinnatifida* and only two in *L. obtusa*; there is therefore a considerable reduction in the number of antheridia formed in a conceptacle in this latter species, though in other respects the structure is substantially the same. It is interesting to note that in *Chondria tenuissima* Grev., a species formerly included in *Laurencia*, the position of the antheridia is entirely different, since they arise all over both surfaces of cellular structures borne on the side branches (Thuret, 1851); there is here no sign of the characteristic conceptacular development of the Laurencieæ, and, working on the grounds of antheridial structure alone, one could fully support the removal of this species to a separate genus.

### (8) POLYSIPHONIA FASTIGIATA* Grev.

Material was obtained from Shanklin, Isle of Wight, and Plymouth in February and April 1924 respectively.

The male plants, which on the south coast are found in the winter and the spring, can be identified in the field by means of their bushy yellow apices, consisting of clusters of antheridia (fig. 17).

The antheridia are produced around specially developed multicellular axes, four to eight of which occur at each apex. In the young plant, where the branching exhibits apparent dichotomy, each branch is terminated by a single apical cell. On the formation of the antheridial axes, these apical cells divide longitudinally several times, each cell thus formed constituting the initial for the fertile axis. From each of these initials, six or eight cells are cut off in a single row; the cell-walls are all gelatinous in character and form a resistant "cuticle" around the axis.

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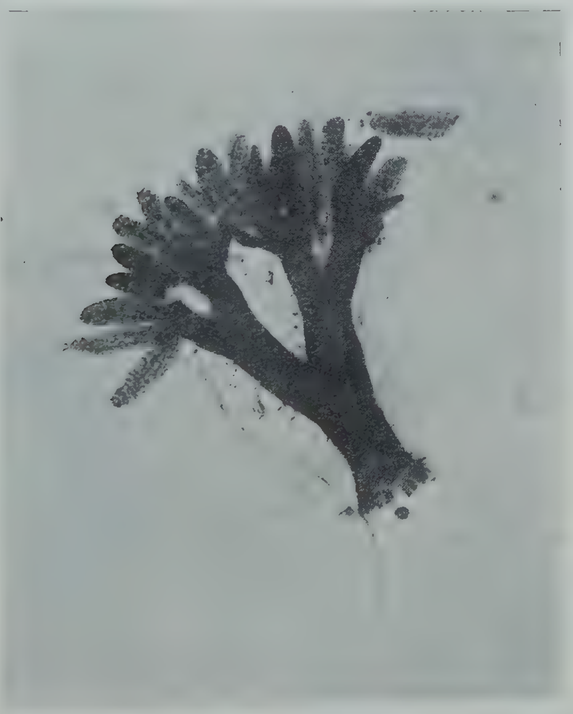
* The presence of antheridia in this species has been noted by many, among them Ellis (1767), Lightfoot (1777), Thuret (1855), and Buffham (1884). No detailed description exists.

All these axes become fertile, none forming sterile hairs as in *Polysiphonia nigrescens* (Kylin, 1922). The two basal cells of the axis do not develop further, but from the remainder a variable number of pericentral cells are cut off, approximately eight to each mother-cell. From these there are then cut off laterally several antheridial mother-cells connected to one another by protoplasmic threads (fig. 18 *a*). The cells are so closely packed together that their swollen walls are fused laterally, while the whole is still clothed externally by the solid common gelatinous investment, often infested with minute epiphytic filaments and diatoms.

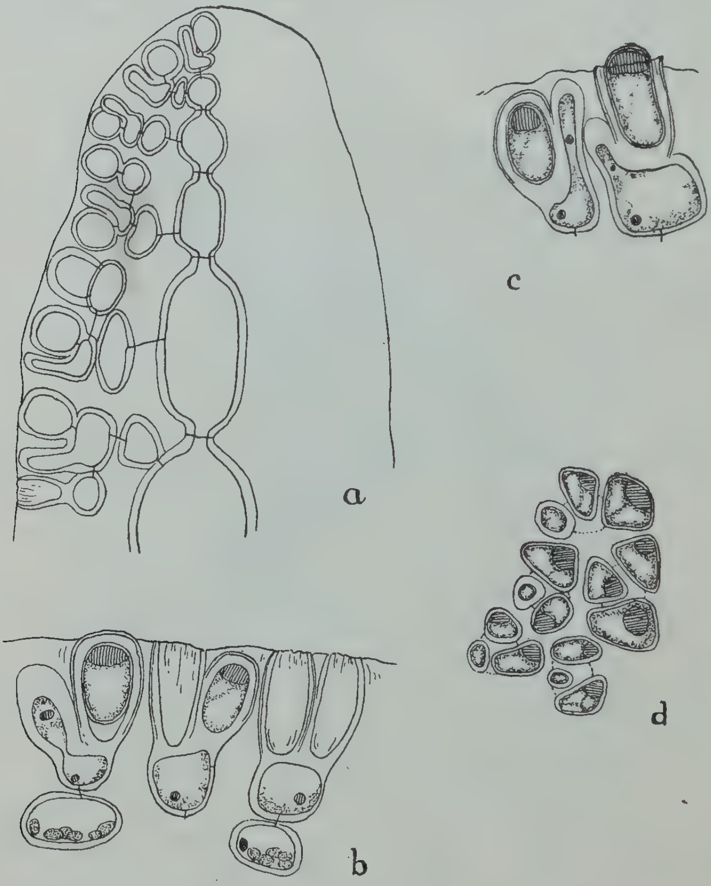
FIG. 17.



Photomicrograph of the apex of *Polysiphonia fastigiata* bearing clusters of ripe antheridia. × 50.

The antheridia develop as protoplasmic protuberances from the mother-cell. The first antheridium arises laterally as a narrow outgrowth forcing up the layer around the mother-cell through the common "cuticle." The contents are abstricted by the ingrowth of the surrounding wall, and when ripe lie as a nearly spherical body within the antheridial wall (fig. 18 *b*). This latter shows two distinct layers, an outer denser one and a middle swollen one, while around the spermatium is a clear refractive area (fig. 18 *b* & *c*). On the escape of the spermatium this area is seen without

FIG. 18.



Antheridial development in *Polysiphonia fastigiata*. All × 1200.

*a.* Part of a longitudinal section of an antheridial cluster, showing the central axis, pericentral cells, and antheridial mother-cells giving rise to antheridia at the periphery.

*b* & *c.* Stages in the development of antheridia.

*d.* Part of an antheridial cluster seen from above; antheridia are in groups of three.

doubt to be a delicate wall enclosing the contents. It is noticeable that these areas are not present when the antheridium it still young, but only become visible as the body attains maturity. When in this position the antheridium has increased in length to such an extent that it has now pierced the "cuticle" (fig. 18 *b*); the wall then splits at the apex and liberates through the aperture the whole contents as a single rounded body.

Meanwhile both a second and third lateral antheridium have been developing from the apex of the mother-cell, following the same stages (fig. 18 *d*). By the time these are mature, the first spermatium has escaped, and the mother-cell then exhibits one empty antheridial sheath and two mature antheridia enclosing spermatia. These are then discharged successively.

The difficulties of technique in dealing with the antheridia of *Polysiphonia* are so great that it is difficult to say whether secondary antheridia are developed in the place of the primary ones. It is, as explained above, impossible to employ microtomed sections, since in them no walls can be clearly made out; hand sections or an examination of the whole cluster is necessary, and even then it is not easy to determine whether an observed spermatium is a primary or secondary one. However, in some clusters where spermatia have not yet been all discharged, it is possible to find single empty sheaths which are the walls of the primary antheridia, and within them there is apparently no sign of a new upgrowing antheridium (fig. 18 *b*). This would point to there being no production of secondary antheridia, a conclusion hardly to be expected, since the secondary development is so common in the Florideæ; on the other hand, it has never been noted for any species of *Polysiphonia*.

The cytology of this species appears to follow the usual course exhibited by members of the higher Florideæ, such as that already described for *Laurencia pinnatifida* (p. 205). The mother-cell is only slightly pigmented and is uninucleate, the nucleus moving to the base of each antheridium and there dividing. The daughter nucleus, which passes into the spermatium, moves to the apex, where it remains suspended by a small amount of cytoplasm above the central vacuole. Details are difficult to make out, but sufficient could be seen to show that the nucleus is in prophase at this time, though the granules could not be counted. The spermatium on liberation is large and measures about 9 by 5 $\mu$, while the nucleus is 2 to 3 $\mu$ in diameter.

### (9) POLYSIPHONIA VIOLACEA * Grev.

Material was collected by Dr. E. M. Delf in August 1924 at Sark.

The antheridia are developed in pale yellow clusters at the apices of the filaments; to the whole cluster Yamanouchi gave the name of an "antheridium," calling the escaping cells "sperms." Each cluster is in reality a short branch, every cell of which, with the exception of the two lowermost, is fertile. The two sterile cells form the stalk, the upper one giving rise to a sterile hair, often branched (fig. 19).

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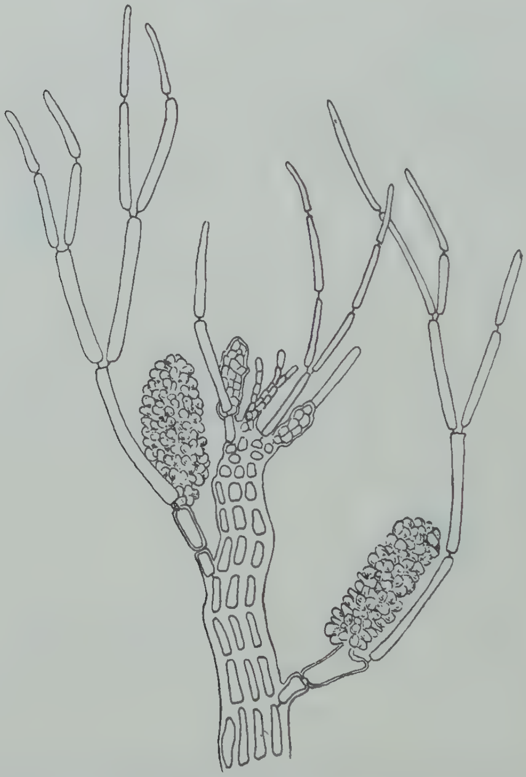
* Antheridia are described by Yamanouchi (1906, p. 409) and mentioned by Rosenvinge (1923).

In the development of the antheridial cluster, Yamanouchi states that the central axis "becomes surrounded and covered by a number of small cells"; these are the pericentral cells, and each one is said to subtend a single antheridial mother-cell, though appearances suggest that more than one is borne by each pericentral cell, as in the case of *P. fastigiata*. The mother-cells when mature are not so closely packed as in the latter species, and it is therefore easier in some ways to make out the structure.

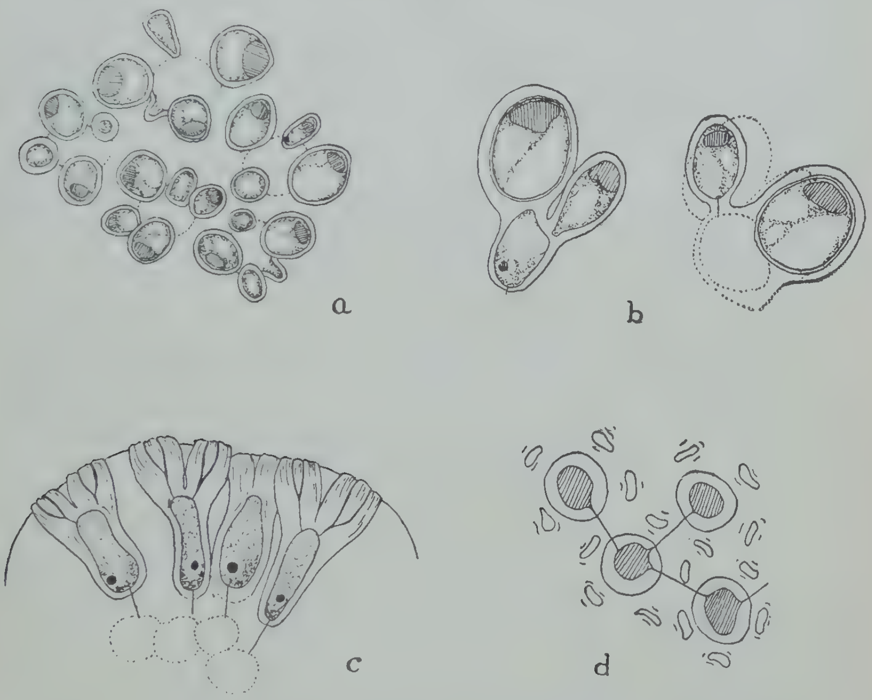
Fig. 19.



Part of the apex of an antheridial plant of *Polysiphonia violacea*, showing antheridial clusters with the accompanying sterile hairs. × 70.

The antheridia are produced as the result of a lateral elongation of the mother-cell. This elongation is surrounded throughout by the gelatinous wall of the latter (fig. 20 *b*), though this, of course, cannot be seen in a microtomed section (cp. Yamanouchi's figures, 1906, pl. 22. figs. 62–81). While still short and narrow the young antheridium is abstricted at the base by the ingrowth of the surrounding wall. It then increases greatly in size, swelling and becoming spherical, the wall at this stage showing two layers, the inner one being strongly marked and separated from the central protoplast by a clear refractive area. The antheridia are borne around the periphery of the outer surface of the flat-topped mother-cell (fig. 20 *a*); this can clearly be seen if viewed from above, when the antheridia appear to be level with the apex of the mother-cell. Such a surface view of the structure was apparently not seen by Yamanouchi, or he could hardly have stated that only two or three antheridia were produced from each mother-cell, since four (or sometimes five) primary antheridia can regularly be seen (fig. 20 *a*). The arrangement of these four is perfect in detail, for one can see that the second always arises at the opposite corner to the first, the third and the fourth developing between them (fig. 20 *a*); in this way space

Fig. 20.



The development of antheridia in *Polysiphonia violacea*.

*a*. Surface view of an antheridial cluster, with the antheridia in groups of four and five around the mother-cells (dotted). × 1200.

*b*. Mother-cell bearing antheridia, seen at two different foci. × 1800.

*c*. Periphery of an antheridial cluster, showing the empty sheaths after the escape of the spermatia. × 1800.

*d*. Surface view of an old antheridial cluster, showing the mother-cells surrounded by apertures through which the spermatia have escaped. × 1800.

is allowed for the first two antheridia to swell and discharge their contents before the alternating two have fully developed. The resemblance at this stage to a four-spored basidium cannot fail to strike the observer, particularly since the spermatia until quite ripe are attached to the mother-cell by a protoplasmic extension, which after the release of the spermatium remains as a short projection similar to a sterigma. Liberation of the spermatium takes place without doubt by means of a split in the apex of the antheridial wall, which by now has stretched to the periphery of the surrounding "cuticle" (fig. 20 *c*), a point entirely overlooked by Yamanouchi, who concluded from his study of microtomed sections that the whole body was cut off and liberated as one (pl. 22. figs. 72, 73). In an old antheridial cluster it is possible with a high magnification and very carefully adjusted illumination to see the "cuticle" traversed in every direction by wrinkled, empty antheridial sheaths (fig. 20 *c*), still showing a swollen outer layer and a more deeply-staining inner region. Evidently the pressure exerted by the spermatium in exit upon the resistant "cuticle" is great, for in surface view each mother-cell can be seen to be surrounded by four, or sometimes five, little pores or slits leading to the empty sheaths below, each pore being much smaller than the diameter of a spermatium and having apparently contracted after the liberation of the latter (fig. 20 *d*). The spermatia when free measure about 7 to 9 $\mu$ in diameter ; the contents, consisting of a single nucleus suspended by strands of cytoplasm above a large vacuole, are surrounded by a very delicate wall. No evidence was obtained that secondary antheridia are formed ; clusters can be found with the mother-cells in the upper regions entirely surrounded by empty primary antheridial sheaths, while in the lower part the primary spermatia are still being discharged. There is no sign in the upper region in these cases that further antheridial development will ever occur (fig. 20 *d*).

The cytology of the antheridia has not been re-investigated.

Although the genus *Polysiphonia* is so widespread, detailed descriptions of the antheridia exist only in three cases—those of *P. violacea* (Yamanouchi, 1906), *P. nigrescens* (Kylin, 1922), and *P. fastigiata* (this paper). In each case the general position and structure of the antheridia agree, though there is some difference as to details. Antheridia in the whole genus appear to be developed in terminal, subterminal, or lateral clusters, these usually being modified hairs. In the three described species the fertile axis of the cluster is subtended by two cells which remain sterile and may produce axillary branches. Around the axis, pericentral cells are formed in varying numbers, giving rise by division to one or more mother-cells which in all cases are small, uninucleate, and colourless, or only slightly pigmented. In *P. nigrescens* Kylin's account implies that another row of cells is interposed between the antheridial mother-cells and the pericentral cells, the latter being comparatively few in number. It is, however, in the descriptions given of the production of the spermatia that the details fail to agree. According to Yamanouchi, two or possibly three "sperms" are constricted off obliquely from the mother-cell in *P. violacea*, and even in discharge they "retain the parent cell-wall." The development in *P. nigrescens* is said by Kylin to be similar to that which he had previously described for *Rhodomela virgata* (1914). In this he definitely states that the spermatium escapes out of its surrounding sheath, this being left behind on the plant. The empty antheridial wall is not, however, figured either for *Rhodomela* or *P. nigrescens* (1922, fig. 77 *c*, *d*), the figures for the latter leaving one to presume that the whole antheridium is cut off as a single separate cell. It is true that in any species of *Polysiphonia* empty antheridial walls would be difficult to see owing to the thick surrounding "cuticle," but in both *P. fastigiata* and *P. violacea* they can be made out with certainty when the magnified structure is examined in a suitable light. In view of the fact that the *discharge* of the spermatium from the antheridium seems to be the usual method of liberation in the Florideæ and not the cutting off of the whole body, it would be of special interest if any species of *Polysiphonia* differed in this respect.

(10) GRIFFITHSIA CORALLINA * (Lightft.) Ag.

Material consisted of two plants gathered on Shanklin Ledge, February 1924.

The antheridial fronds can be recognized in the field and easily distinguished from other fertile material of this species. Those gathered were small—not more than 2·5 cm. in height—though apparently fully developed; on them the antheridia are visible as colourless areas encircling the upper constrictions of the articulations (fig. 21), these paler regions forming a striking contrast to the otherwise deep red colour of the plant. The antheridia occur only at the younger nodes, forming whorls around the second, third, and fourth constrictions (fig. 21). The thallus, which is attached basally by means of creeping rhizoids, is dichotomously branched at irregular intervals, and is made up of single rows of elongated inflated cells from 1 to 2 mm. in length; these are multinucleate, with the nuclei and small round plastids arranged around the periphery. The whole is enclosed in a very thick two-layered gelatinous "cuticle," which is visible to the naked eye and imparts to the thallus its characteristic slimy feeling; the inner layer is thin and delicate, sheathing the cells; the outer one thick and resistant. This "cuticle" is contracted and thinner at the nodes.

The antheridia are borne at the apices of long richly-branched axes, extending at right angles to the surface of the thallus, and united by the gelatinous matrix in which they are embedded. An antheridial axis first appears as a single cell which apparently arises as a protuberance from a thallus cell. In the earliest stages shown by the material the axis is represented by a large round uninucleate cell connected with the thallus by an elongated gelatinous wall (fig. 23 *a*). From this, six to eight cells one above the other are cut off, more or less in a straight row, forming the central axis of the antheridial branch (fig. 23 *c*). These increase greatly in size, becoming multinucleate and when mature containing as many as ten to twelve nuclei (fig. 22); the antheridial branch is approximately ·1 mm. in length (fig. 22). Meanwhile around each of these central cells a number of pericentral cells have been cut off in every direction, often as many as ten to twelve being formed from each main cell, each containing two to three nuclei (fig. 23 *b*). From the pericentral cells are cut off a further series of cells, many of which grow out into short branches bearing at their apices antheridial mother-cells, others however by their next division giving rise to immediately mother-cells (fig. 22). At the same time it is to be noted that occasionally antheridial mother-cells arise directly upon the pericentral cells, or even, in the younger regions, upon the central cells, though Kylin does not mention this in his short description; both the mother-cells and the antheridia are uninucleate (fig. 22). All these cells, with the exception of the antheridia are pigmented, but in nearly every case such

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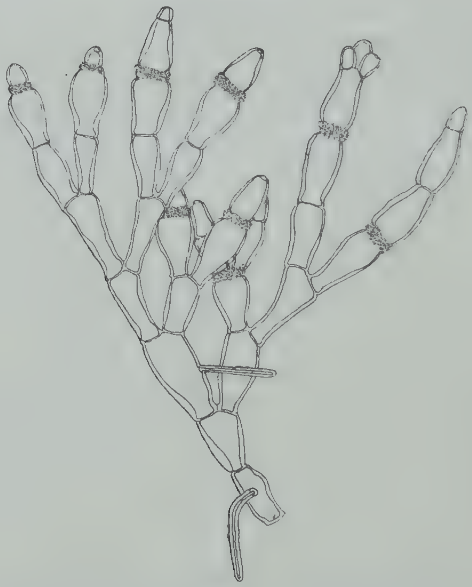
* The presence of antheridia is mentioned by Thuret (1855) and Buffham (1884). Guignard (1889) and Kylin (1916 *a*) give short descriptions of the structure.

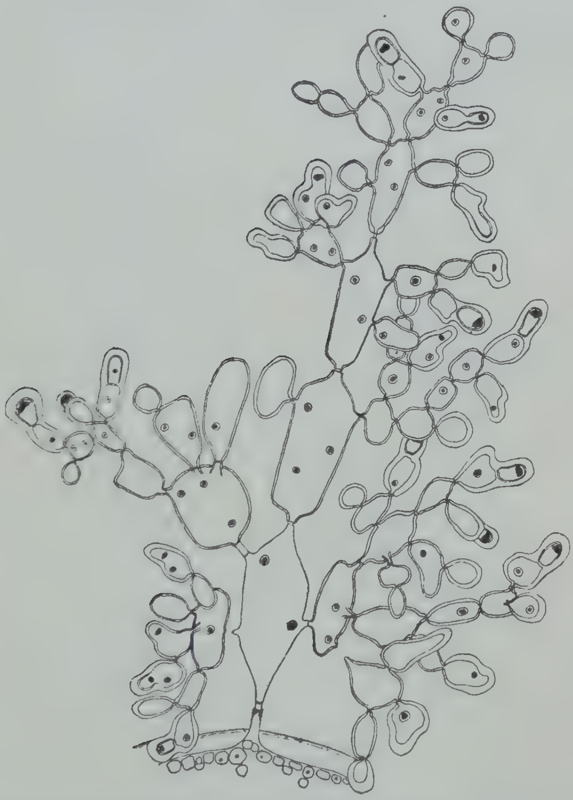
Fig. 21.



Portion of an antheridial plant of *Griffithsia corallina*, showing the position of the antheridial filaments. × 6.

dense granular contents are present that the position of the plastids and, to some extent of the nuclei is obscured. Typically, therefore, each of these antheridial branches consists of a distinctive central axis surrounded in every direction by pericentral cells, which again in most cases give rise to further cells, on which, sooner or later, the antheridial mother-cells and the antheridia are borne (fig. 22). It is evident that in this somewhat peculiar structure there is no very regular rule of development, but the antheridial mother-cells may be found growing out from central, pericentral or higher orders of cells.

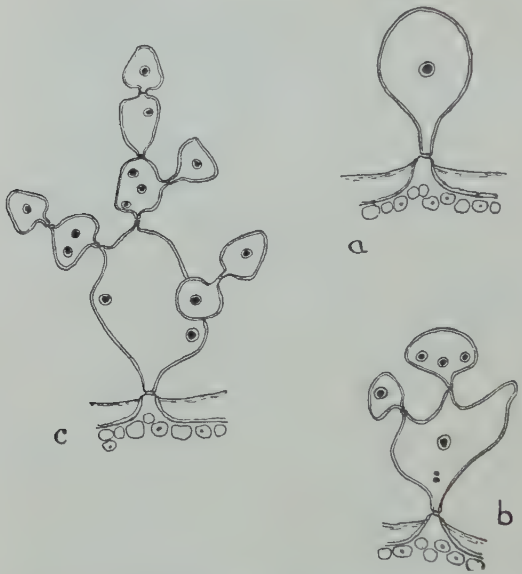
FIG. 22.



Single antheridial branch from a fertile node of *Griffithsia corallina*, showing the attachment to the thallus and the development of lateral axes. × 1200.

The antheridial mother-cells are uninucleate and contain a few poorly-developed plastids, the whole being surrounded by a gelatinous wall which is thicker than that of the other cells of the antheridial branch; like other Floridean cells, these remain in communication with the cell from which they are cut off by means of a protoplasmic connection. Each mother-cell gives rise to two (fig. 24 *b*) and sometimes three (fig. 24 *a*) antheridia. These are formed successively as small colourless sub-terminal projections from the mother-cell, forcing upwards the gelatinous wall (fig. 24 *a*). The projections are abstricted at a point level with the original apex of the mother-cell by the ingrowth of the wall, leaving no apparent protoplasmic connection between the two cells, and the contents then lie as slightly elongated bodies within the young antheridium. When mature, the spermatium, which is formed from the whole contents of the antheridium, consists of a large colourless body, about 6 by 4 $\mu$ in diameter, with an apical nucleus suspended in a little granular cytoplasm, and a large vacuole below; the wall surrounding the whole is very thick and shows signs of layers within it, while immediately around the spermatium is a clear refractive area (fig. 24 *b*). It is impossible to say with certainty at this stage whether this is an empty space in which the spermatium is lying, or whether it represents a very delicate wall surrounding this body; but the latter suggestion is supported by the fact that immediately after the apex of the wall of the antheridium splits and the spermatium is liberated, the latter can be seen in the surrounding medium as a spherical body enclosed in a very delicate but unmistakable gelatinous wall. The question as to whether there is any secondary antheridial development in this species is difficult to decide; Kylin makes no mention of any such development, implying that it does not take place.

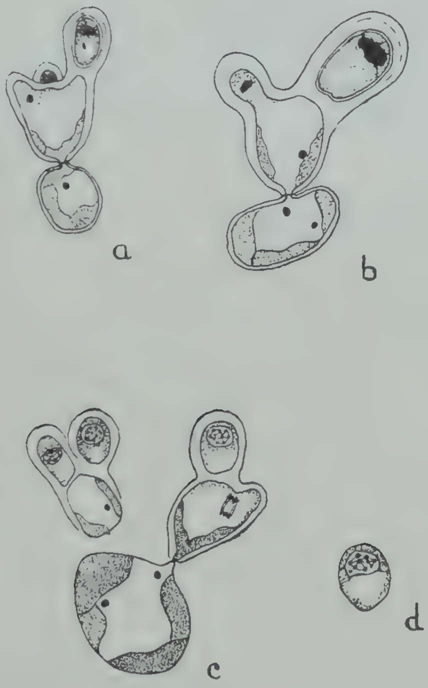
FIG. 23.



Three stages (*a*, *b*, and *c*) in the development of the antheridial axis of *Griffithsia corallina*. Plastids omitted. × 1200.

On the other hand, the only remark that Guignard has to make with regard to this species is that a second antheridium grows up within the sheath of the first, and he illustrates this with a very convincing figure. Unfortunately my material was too young to be decisive, as in only a few cases had the primary spermatium been discharged; there are signs, however, that a secondary antheridium might develop (fig. 24 *a*, right), and in view of the common occurrence of secondary antheridia among the Florideæ one would expect it.

FIG. 24.



Antheridia of *Griffithsia corallina*. × 1800.

*a* & *b*. Hand preparations, showing the development of the antheridia.
*c*. Microtomed sections, showing the nuclear construction of the antheridia and mother-cells.
*d*. Escaped spermatium.

Although the nuclei of the ripe spermatia are small—about 1·9 to 2·2 μ in diameter—yet the details were fairly clear. On the formation of a young antheridium the single small nucleus of the mother-cell moves to the base of the projection and there divides (fig. 24 *c*). The details of this division can be observed, but owing to the small size there is difficulty in counting the number of chromosomes. One daughter nucleus moves upward into the antheridium, the other back into the mother-cell, where it remains until it again passes to the base of another projection. The antheridial nucleus is seen as a large densely-staining body, which during the ripening of the spermatium moves gradually to the apex and is there suspended by very delicate protoplasmic threads. While still in the base of the spermatium, it is difficult to make out any structure, for it either stains a homogeneous deep purple with hæmatoxylin, or else loses the stain altogether. Half-way up the spermatium the nucleus can be seen to consist of very delicate linin threads, at the angles of which are small densely-staining bodies—the granules or "Körnchen." When the nucleus is at the apex, the granules are slightly larger and appear to be about 10 in number; appearances, however, in certain cases suggest that the number is probably greater than this, 13 or 14 being perhaps more correct; the linin network is still present, and though no nucleolus is visible the nuclear membrane can always be seen (fig. 24 *c*). The nucleus is in this condition when the spermatium is liberated (fig. 24 *d*).

### (11) HALURUS EQUISETIFOLIUS * Kütz.

Material was found both attached and among drift at Shanklin, February 1924.

The antheridia appear to develop in the spring in the south of England. The male plants are easily recognizable with the aid of a lens or even with the naked eye, for the antheridia are borne clustered on the incurved ramuli of small, pale pink involucres of whorled branches, which are developed laterally on the lower part of the main stems or branches of the plant; these involucres are conspicuous, and, when examined closely, are seen to have white patches in the centre, caused by the bunches of colourless ripe spermatia (fig. 25).

The vegetative plant of *H. equisetifolius* consists of a main filamentous stem, much branched, both stem and branches being composed of a single row of multinucleate, pigmented cells enclosed, as in *Griffithsia corallina*, in a thick gelatinous "cuticle." The junctions of these cells, more especially in the younger parts of the plant, are densely clothed with whorled filaments, which are incurved and branched; towards the base of the plant the whorled character is lost, and the whole stem appears to be covered indiscriminately with short cellular filaments. On the formation of the antheridial involucre, a thick, nearly colourless, lateral branch arises from a main or lateral stem at the point of departure of an involucre; this branch develops at its apex one or more whorled involucres on which the bunches of antheridia arise (fig. 25).

If any confirmatory evidence of the close relationship between *G. corallina* and *H. equisetifolius* were required, it could be found in the unmistakable similarity of development and construction of the antheridial bunches in the two species, those in *H. equisetifolius* being somewhat smaller and simpler. The antheridial filament arises as a lateral outgrowth from one of the cells of the involucral branches; this outgrowth, which is multinucleate and pigmented, is cut off as a single cell always remaining enclosed in the gelatinous "cuticle" of the vegetative cell and in protoplasmic connection with the latter. By division a short antheridial filament is formed, generally composed of not more than four cells (fig. 26); from these, about four to

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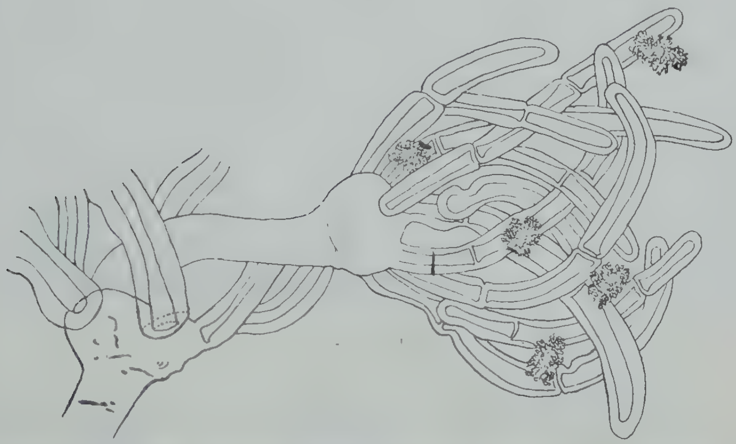
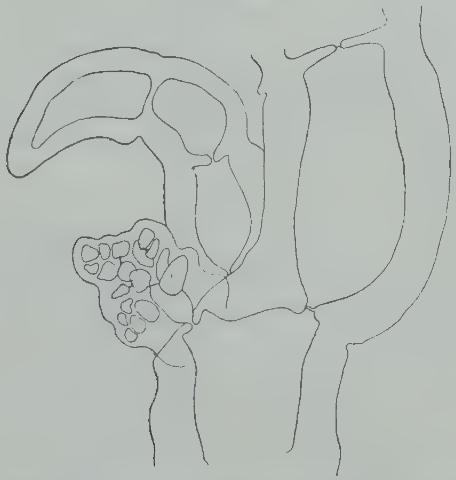
* Antheridia previously noted by Harvey (1849, pl. 67) and Chemin (1923).

FIG. 25.



Outline drawing of a lateral involucre of *Halurus equisetifolius* bearing antheridial branches. The main axis with a whorl of branches is indicated. × 75.

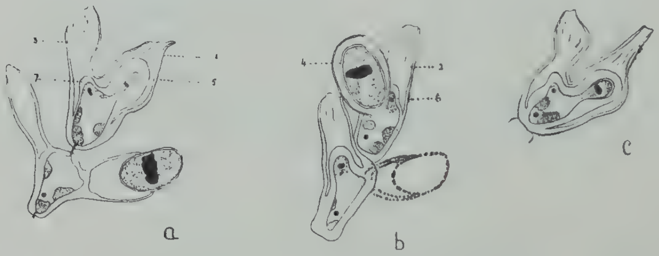
FIG. 26.



Outline drawing of a small portion of a lateral involucre of *H. equisetifolius*, showing a young antheridial bunch in process of development. × 900.

eight lateral cells, apparently always uninucleate, are cut off at right angles all round, and these give rise, by further divisions, to numerous small interlacing branches, composed of short rows of slightly pigmented uninucleate cells, the whole of this structure forming a single bushy antheridial group and measuring about ·08 of a mm. in diameter (fig. 26). Any cell of the lateral branches of this antheridial group appears able to function as a mother-cell and to give rise to antheridia, but only the three or four upper cells generally do so (fig. 27 *a* & *b*). This is in contrast to *G. corallina,* for here only the terminal or lateral cells borne on the filaments become mother-cells, and never the intercalary cells of the filaments; indeed, were the structure not unmistakable in *H. equisetifolius,* one would doubt the point, since in other Florideæ described the antheridial mother-cells appear always to be borne terminally. These mother-cells are very prolific, often giving rise in the normal manner to four primary antheridia, while secondary ones are developed successively within the empty sheaths (fig. 27). The antheridia when first formed are long and narrow, rapidly broadening out and assuming the oval shape, with the large central nucleus suspended by cytoplasmic threads. The antheridial wall is in this case very thick, and when ripe it distinctly shows a definite outer layer (fig. 27 *b*), to which filamentous growths, diatoms, etc. are often firmly attached. Within, there is a clear area around the spermatium, and the latter when issuing from its sheath quite obviously possesses a thin wall. When mature the body is before liberation about $7 \times 4\ \mu$, the nucleus attaining a diameter of approximately $2\ \mu$.

FIG. 27.



The development of antheridia in *Halurus equisetifolius.* × 1800.

*a* & *b*. Drawings at a low and high focus respectively of two terminal cells of an antheridial branch producing successively primary and secondary antheridia. These are numbered in order of development.

*c*. Development of secondary antheridia within the empty sheaths of the primary ones.

The cytological details were difficult to make out, owing to the extremely small size of the nucleus and the difficulties inherent to such filamentous material. No stages in the division of the mother-cell nucleus could be found, though this apparently takes place in the usual manner, and the nucleus of the spermatium was only seen when the latter was about to escape; at that time the nucleus was composed of numerous staining granules about 10 in number, connected by delicate threads.

On comparing the structure of the antheridial filaments and the development of the antheridia in the three species *G. Bornetiana* Farlow (Lewis, 1909) (= *G. globifera* (Harv.) J. Ag)., *G. corallina* (p. 215), and *H. equisetifolius*, one finds that there is a considerable likeness. In all three the antheridia are borne on special antheridial branches, though in one case these filaments are found covering the apices of the terminal cells of the plant (*G. Bornetiana*), in another confined to whorls at the nodes (*G. corallina*), and in the third scattered at random on special involucral branches. The branches are most strongly developed in *G. corallina*, where they grow to be as long as ·1 mm. and are very bushy and interlaced; in *H. equisetifolius* they do not attain to more than ·08 mm., while in *G. Bornetiana*, though no measurements are given, they appear to remain quite small, only being made up of the original primary cell, which buds off secondary cells, from which the mother-cells are directly derived; the bushy interlacing habit is to a large extent lost here. The different positions of the antheridial mother-cells in the two species investigated have already been noted, while in *G. Bornetiana* these are always terminal on the single cell of the secondary branch. The mother-cell in each case produces two or three antheridia, though four occur in *E. equisetifolius*. Secondary antheridia are only definitely noted for the latter species, though probably occurring also in *G. corallina*. No mention of them is made in *G. Bornetiana*; indeed, the figures and descriptions lead one to believe that in this species the whole primary antheridium breaks off and escapes, an assumption which would probably require modification on further investigation. The spermatia, too, are very small in *G. Bornetiana*, being only $3 \times 2\,\mu$; their cytology is unknown.

### (12) CALLITHAMNION BRACHIATUM* Bonnem.

Material was collected from Freshwater, Isle of Wight, April 1923.

Mention has been made in algal literature of the discovery of male plants in no less than 13 species of *Callithamnion*, and in nearly all cases the position of the antheridia as lateral bunches of cells borne on the upper branches has been noted, though in *C. tetricum* they are said to be "almost terminal" (Buffham, 1884), and in the closely related *Ptilothamnion pluma* they are completely terminal on the upper pinnæ. So far as is known, the structure of the collection of antheridia in each species is strikingly similar, always appearing as a more or less spherical bunch of small cells gathered round a pedicel, while from the outermost ones colourless bodies escape.

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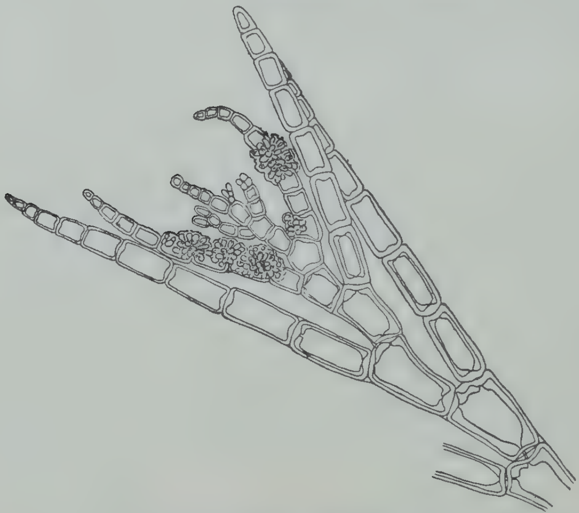
* Thuret (1855) first saw antheridia in this species, and Buffham (1884) gave a slight description of them.

The groups of antheridia of *Callithamnion brachiatum* do not, at first sight at any rate, appear to show any serious deviation from what may be regarded as the normal construction in the genus. The bunches of pale cells are situated laterally on the upper crowded branches which terminate each shoot (fig. 28). Often every cell can be seen giving rise to clusters, the youngest of these being nearest to the pointed apex of the branch (fig. 29). At other times only a single bunch of antheridia will be found on a branch, and possibly no others near it. A mature cluster measures approximately 40 $\mu$ in diameter, and in consequence of its small size and the absence of other distinguishing features it is impossible to detect the antheridial plants without the aid of a microscope. To the difficulty of ready recognition may possibly be due the apparent scarcity of the plants, though this may also be partially accounted for by the probability that after discharging their function the useless antheridial bunches fall off and the plants appear to be sterile. At the same time, there is some ground for thinking that fewer male plants are actually developed than either female or tetrasporic. In connection with this it is interesting to note that antheridia in this genus only appear to be found, at any rate on the south coast, from April to September. Such statements as exist, record the presence of spermatia in April and August, but it is not clear whether there are two distinct seasons of development—spring and autumn—or whether the antheridia are produced throughout the whole summer.

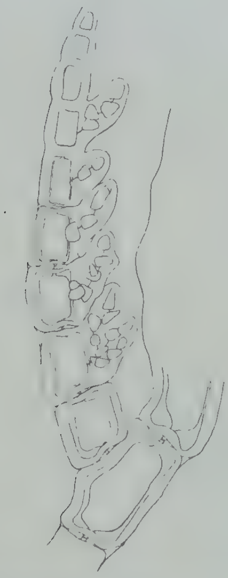
FIG. 28.



Outline drawing of a group of terminal pinnæ of *Callithamnion brachiatum* bearing antheridial bunches. × 225.

On close examination the bunches of antheridia in *G. brachiatum* are seen to exhibit a definite structure, for they are each borne on a pedicel composed of three or four cells, the basal one of which is larger than the others, and therefore more conspicuous. This pedicel arises, like the main axis in *Halurus equisetifolius*, as a single cell, cut off laterally from a cell of the vegetative branch and enclosed in the common gelatinous wall of the latter (fig. 29); in some cases a vegetative cell may give rise to two of these pedicel cells, and two bunches of antheridia are then developed. The basal pedicel cell then divides transversely, giving a row of three to four cells forming the main axis of the bunch, and each of these cuts off around it about four cells (fig. 29); these are, of course, always in protoplasmic connection with the central axis. The secondary cells divide at least once by a transverse wall and sometimes twice, giving very short branches of two to three cells, the terminal ones forming the antheridial mother-cells (fig. 30 *a*). The whole of this structure is enclosed in a common gelationous wall derived from the original vegetative cell.

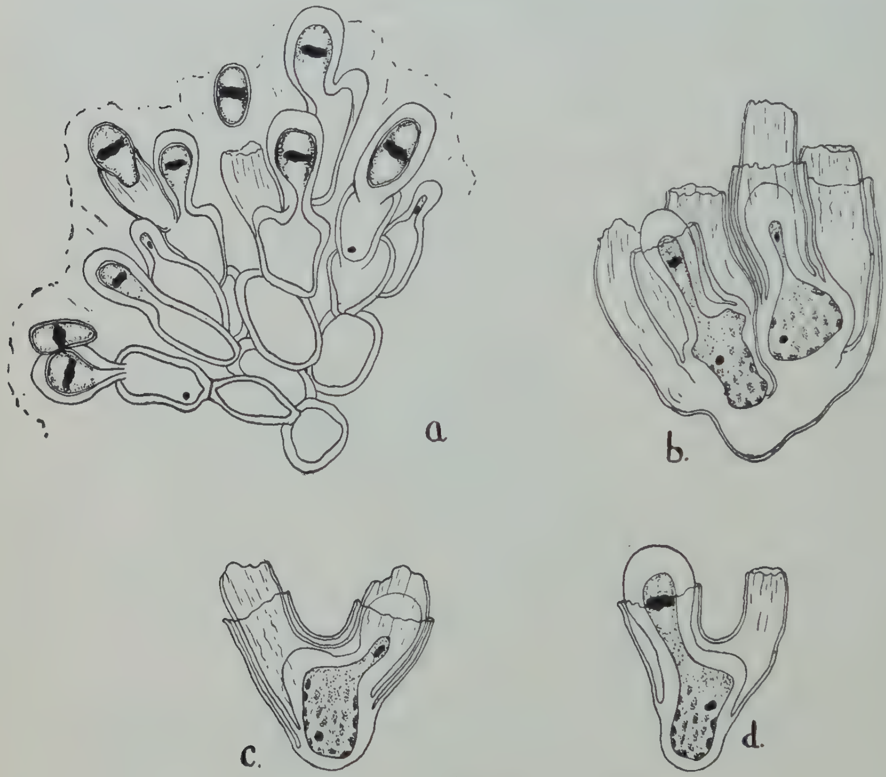
Fig. 29.



Outline drawing of a branch at the apex of a shoot of *Callithamnion brachiatum*, showing stages in the development of bunches of antheridia. × 750.

The antheridial mother-cells are, in appearance, very similar to the other cells of these small branches, except for the somewhat thicker gelatinous walls at the apex. Each mother-cell puts out a thin narrow protuberance, forcing up its wall (fig. 30); this protuberance is abstricted by the ingrowth of the wall at the base, and the first antheridium thus formed is an elongated body with protoplasmic contents, much swollen at one end and pulled out to a tail at the other, the whole being enclosed by a very thick two-layered wall. Gradually the antheridial contents become rounded off and swollen ; the wall shows signs of strain ; a split appears at the apex, and through the hole the spermatium escapes, passing through the surrounding thin gelatinous matrix. No sign was seen of the little caps described and figured by Guignard for *C. roseum* (1889, pl. 6. fig. 2) and said to open at the apex of the antheridium, allowing the spermatium to escape. The spermatium, which immediately after liberation is about $3 \times 5\,\mu$ in size, is surrounded, at any rate when free, by an exceedingly delicate refractive wall (fig. 30 *a*). The

Fig. 30.



Development of antheridia of *Callithamnion brachiatum*. × 1800.

*a*. Part of an antheridial bunch pressed flat by the weight of the cover-glass.
*b*. Two antheridial mother-cells, each with three sets of empty antheridial sheaths. Secondary (left) and tertiary (right) antheridia developing.
*c*. Antheridial mother-cell giving rise to a tertiary antheridium.
*d*. Formation of a secondary antheridium.

tough antheridial wall is either left standing as a sheath, or, when the strain is released, it springs back and is seen as a wrinkled collar above the mother-cell (fig. 30 *d*). This production of primary antheridia is repeated three times from different points around the apex of most mother-cells (fig. 30 *b*); in some cases only two primary antheridia appear to be present, but it is probable that this impression is due to the impossibility of cutting hand-sections and to the antheridia overlying one another. Immediately following the production of primary antheridia, the development of the secondary ones takes place in exactly the same sequence as was followed by the first. Within the empty antheridial sheath grows up a small protuberance, enclosed in a thick gelatinous wall (fig. 30 *d*); this soon extends beyond the shrunken sheath, which appears as a collar around its base, and the spermatium ripens rapidly and is discharged as before. Clear evidence was also obtained in this species that a third crop of antheridia is developed within the empty sheaths of the two previous (fig. 30 *c*); tertiary antheridia, though sometimes suspected, have not been noted in any other species of the higher Florideæ to the writer's knowledge. No sign of more than three sheaths, one within the other, could be found (fig. 30 *c*).

It is quite evident that, apart from minute details, the nuclear structures follow the usual course of behaviour. Apparently each cell of the antheridial bunch contains a single nucleus. In the antheridial mother-cell this can be seen to move to the base of each protuberance, and there presumably it divides, since a single nucleus is found in each young antheridium, and the mother-cell nucleus has returned to the base of the cell. In the ripe spermatium the nucleus is about 2 to 3 $\mu$ in diameter, and while still retained in the antheridium, it forms a band across the centre, being suspended in this position by strands of cytoplasm which surround a large vacuole. When, on liberation, the spermatium becomes spherical, the nucleus has a completely central position. Of the internal structure of the nucleus, no details can be seen without microtomed sections, and these, owing to shortage of material, were not available. The pigment present in the cells of the branches which subtend the antheridia is very slight, though plastids can be observed; the whole structure has, when fresh, a very pale pink appearance; in the antheridial mother-cells the pigment is almost lacking, and in the antheridia there is none.

The resemblances between the bunches of antheridia in *Callithamnion*, *Griffithsia*, and *Halurus* could hardly be overlooked. In all cases the antheridial bunches arise as lateral outgrowths from vegetative cells and take the form of a central axis surrounded by secondary branches. In *G. Bornetiana* (Lewis, 1909) this axis is said to be reduced to a single cell, bearing the secondary branches at its apex; in the species of *Callithamnion* above described it consists of three to four cells, and in *G. corallina*, *G. setacea* (Thuret, 1851), and *H. equisetifolius* of a large number. The branches vary in length, in *Griffithsia Bornetiana* often consisting only of the single antheridial mother-cell, in *Callithamnion brachiatum* having one or two cells interposed between this and the main axis, and in the other two species of *Griffithsia* and *H. equisetifolius* being composed of a considerable number. The whole of this bushy structure appears to be, in each case, embedded in a gelatinous matrix derived from the gelatinous walls of the vegetative cells. Secondary antheridia probably occur in all the above-mentioned species, though there is no record of their development in *G. Bornetiana*. Such striking similarities as shown in these two genera form a satisfactory corroboration of a relationship which was originally recognized on the grounds of the structure of the vegetative organs and the similarity in cystocarpic development.

### (13) CERAMIUM RUBRUM * Ag.

Material was collected at Wembury Reef and Bovisand Bay, near Plymouth, April 1924.

The spermatia are borne on the surface of the radial thallus branches; they occur apparently in large numbers, but in spite of this they do not appear to impart any distinctive character to the plant by means of which it can be recognized with the naked eye. When slightly magnified, branches bearing spermatia are seen to be fringed with a colourless edge, owing to the projection of the unpigmented antheridia (fig. 32 *d*).

In order to understand the relation of these antheridia to the tissues of the thallus, it is necessary to consider the vegetative structure of the mature plant (fig. 31 *a* & *b*). This consists of a central axis of swollen cells, each approximately 1·0 to 1·1 mm. long and much the same in diameter. These cells are contracted at their points of junction (*i. e.* the "nodes"), while closely applied to the wall are curiously elongated plastids (fig. 31 *a*). Surrounding this axis is a layer of pericentral cells; these are much elongated in the internodes, extending the length of a single axial cell and branching sparingly; at the nodes they are more nearly isodiametric and often two layers in thickness. Externally lie the cortical cells enclosed in a gelatinous "cuticle." These cells are roughly isodiametric and very irregular in form and position; at the nodes of the articulations they are regularly two cells deep in cross-section, but in the internodes they are only occasionally so, and, indeed, are somewhat widely separated from one another, thus giving an indication of the connection with those species where the cortication clothes only the nodal area of the articulations (i. e. *C. diaphanum* Roth, *C. acanthonotum* Carm., etc.).

In the younger regions of fertile portions of the thallus, practically every peripheral cell appears to give rise to antheridial mother-cells, though in older portions these become limited to definite areas (fig. 32 *d*) as in *Ceramium diaphanum*, where, according to Buffham (1884), the antheridia are entirely confined to the corticated nodal regions.

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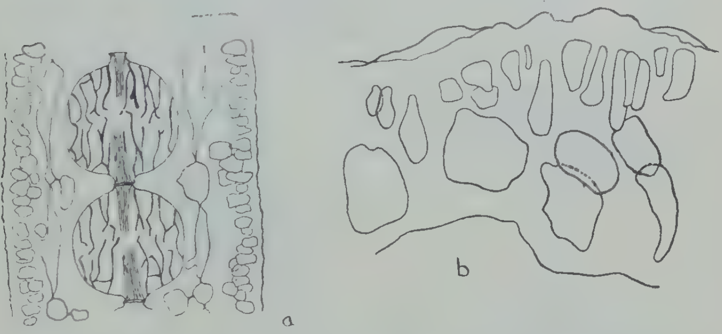
* Thuret (1855) first recorded the antheridial plants, while Petersen (1908) notes he has found "a small number of antheridia."

In a paragraph on the development of the antheridia in the Ceramiaceæ as a whole, Petersen (1908) states that in the few cases (four) where he has been able to observe the formation of the male cells it is always preceded by the continual division of the cortical cells. This certainly occurs in *C. rubrum*, though the divisions are very irregular in number. They apparently consist first in the formation of periclinal walls in the peripheral cortical cells, followed by anticlinal walls in the outer cells thus cut off, dividing these into several smaller ones which form the mother-cells. No definite number of mother-cells are formed from a cortical cell, three, four, or even five being found. Each mother-cell contains a single nucleus and is pigmented.

Fig. 31.

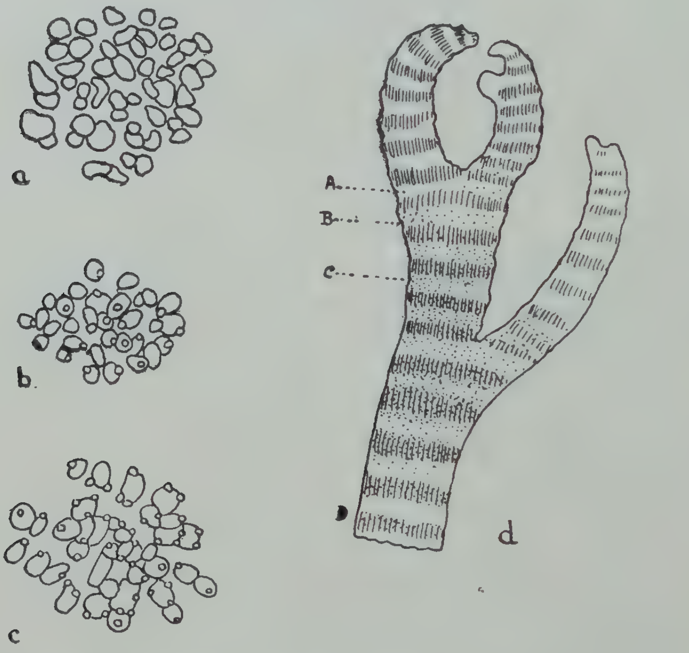


*a*. Longitudinal section through two internodes of a vegetative thallus of *Ceramium rubrum*, showing the central, pericentral, and cortical cells. × 350.

*b*. Transverse section through an internode. × 750.

Even a superficial view of the fertile male frond gives a clear indication of the method of antheridial development. In fig. 32 *d* at the region A (enlarged in fig. 32 *a*) the antheridial mother-cells are seen as an irregular layer covering the surface of the frond. At a slightly lower level, B, a region (enlarged in fig. 32 *b*) is reached where these, viewed from above, are each seen to have given rise to a small cell which appears to be seated on their upper surface; sections show that this is the first antheridium which has been formed as an outgrowth on the surface of the cell. At C (enlarged in fig. 32 *c*) each original mother-cell is seen to have two or three clear circular areas on its surface, and these represent the two or three antheridia which appear to be budded off at first from the mother-cell. Thus the formation of antheridia takes place on the upper portions of the frond in regular acropetal succession. In section (fig. 33 *a* & *b*) it is seen that the formation of the antheridia is preceded by a slight elongation of the mother-cells towards the exterior of the frond. From each of these elongated cells arises a small subterminal protuberance piercing the gelatinous "cuticle"; the latter does not peel off as in *Rhodymenia palmata*, but remains clothing the thallus, and is pierced in every direction by the rounded apices of rapidly-growing projections (fig. 33 *c*). During its growth these are covered by a gelatinous wall, which increases greatly in thickness at the apex and later becomes the antheridial wall. When each projection has attained a length approximating to that of the mother-cell, the contents are abstricted by the ring-like ingrowth of the gelatinous wall, which, when completed, is curved upwards in the centre (cp. fig. 33 *a*). The constriction does not, however, take place at the point of attachment of the projection to the mother-cell, but a short distance above, leaving about a third of the projection attached as a blunt outgrowth to the mother-cell (fig. 33 *a*). The upper portion, which has been detached by abstriction, forms the antheridium, consisting

FIG. 32.

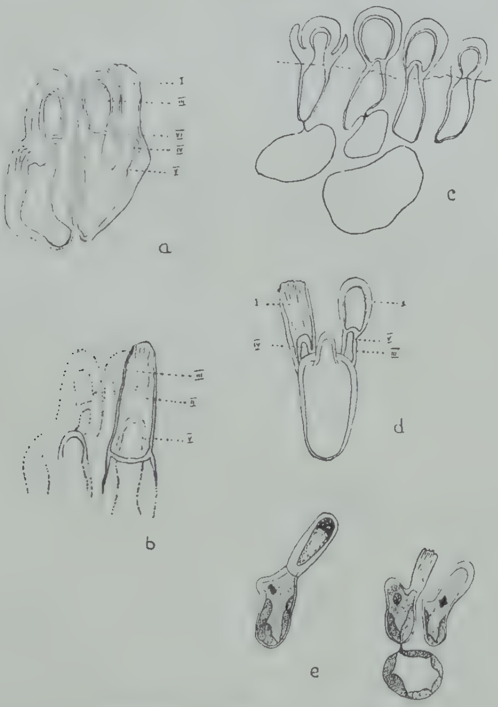


Development of antheridia in *Ceramium rubrum*. *a–c*, × 750; *d*, × 100.

*a.* Surface view of A in fig. *d*. Antheridial mother-cells.
*b.* " " B " Appearance of first antheridia on mother-cells.
*c.* " " C " Appearance of second and third antheridia.
*d.* Portion of young thallus, showing distribution of antheridia (stippled) both on nodal (shaded) and internodal regions.

of an outer wall and cytoplasm surrounding a single nucleus. The contents become rounded, and appear to be separated by a clear area from the outer wall. The antheridium is now ripe, and the whole contents are ready to be extruded as a single spermatium. This has been observed to take place in fresh material by means of a split in the apex of the antheridial wall, the latter being left behind as an empty shrivelled sheath when the single thin-walled spermatium has slipped out (fig. 33 *a*). The size of this body at the moment of extrusion is from 8 to 9 $\mu$ in length and about 4 $\mu$ in breadth.

FIG. 33.



*Ceramium rubrum.* All × 1800.

*a,* low focus, and *b,* high focus of an optical section showing the production of antheridia from the mother-cell. Right—the antheridia are numbered in order of development.

*c.* Optical section showing the position of the antheridia with respect to the cuticle.

*d.* Imaginary solid view of the antheridial mother-cell. Antheridia numbered in order of development.

*e.* Microtomed section through a mother-cell, showing the division of the nucleus.

Meanwhile another sub-terminal projection has been growing out from the antheridial mother-cell, and this, following the above course of development, forms the second antheridium. Before the discharge of the second spermatium a third projection arises, and similarly develops into a third antheridium. The position of these three successively developed antheridia is best seen in the diagram shown in fig. 33 *d*, where the mother-cell is depicted in stereoscopic view, the antheridia in three successive stages of development standing around its dome-shaped apex. The same realization of the position of the antheridia is gained from fig. 33 *a* & *b*, where a mother-cell with its antheridia is observed first at a low focus and then at a high one.

It seems, however, clear that the number of antheridia developed from one mother-cell is not limited to three, for in regular order a new antheridium is seen arising within the empty wall of each old one (fig. 33 *a*–*c*). This occurs by the development of the small projection left at the base of each antheridium at the moment when the first one is constricted off. This projection grows upward, covered by its gelatinous wall (fig. 33 *b*, left), and is finally abstricted, the contents then escaping and two empty antheridial walls are left behind, one within the other. The reproductive capacity of the mother-cell appears to be exhausted when six antheridia have been produced in this way, for a third antheridium growing up in the same position as the two previous ones has not been observed. One of the most striking facts about the development of these six antheridia from a single mother-cell is the very regular manner in which it takes place (fig. 33 *d*), no overlapping in the discharge of spermatia from one mother-cell occurring. Presumably this method of successive discharge affords a far greater possibility of some at least of the bodies fulfilling their function than if all were cast into the sea at the same moment and under the same conditions.

Considerable difficulty was experienced in observing the smaller cytological details, for although the material was subjected to the same fixing and embedding processes, yet the nuclear details after microtoming were far from being as distinct as in *Laurencia* or *Chondrus*—a fact which may partly be due to the susceptible character of the material with regard to shrinkage.

Apparently the pericentral cells are multinucleate, but the peripheral cells and later the antheridial mother-cells have each only one nucleus. These latter cells contain numerous plastids, none of which, however, appears to pass into the antheridium (fig. 33 *e*). On the formation of the latter the nucleus of the mother-cell, which in the resting position is central or basal, passes up to the base of the projection and there divides (fig. 33 *e*). The daughter nucleus passes into the young antheridium, and by the time the latter is mature occupies the characteristic curved apical position ; this behaviour occurs at the formation of each antheridium. The spermatial nucleus at the time of the extrusion of the spermatium is in prophase, and shows a number of typical "Körnchen" or granules ; it was impossible to count these with any certainty, but there appear to be from six to eight present in each nucleus. When the spermatium is extruded it is an oval body, the blunt apex being occupied by the large nucleus (about 3 $\mu$ in longest diameter), while around there is a small amount of vacuolate cytoplasm enclosing a large central vacuole.

### (14) DUMONTIA FILIFORMIS * Grev.

Material was gathered at Wembury Bay (Plymouth) and Looe in April 1924.

As a result of collecting between February and July, Dunn * came to the conclusion that antheridial plants are, at South Harpswell, Maine, fertile only for two to three weeks in April. The antheridia are developed in some cases over almost the whole of the thallus with the exception of the base of the stipe and the hapteron. More often, however, sterile patches are left among the sheets of antheridia, dividing these into irregular sori, especially at the apex.

The thallus is composed of three regions: an inner one of long hyphal cells known as the medullary hyphæ, which on the exterior give rise to larger and smaller sub-cortical cells. Dunn states that the cells of this outer layer (which are only slightly pigmented) become the antheridial mother-cells; in other words, these latter are homologous with the outer cortical cells of the tetrasporic or cystocarpic plants. It is difficult to make this comparison since sterile regions of male plants are not easy to find, but on examining the structure at the base of the stipe where there are as yet no signs of antheridia, and that of the sorus above, it is seen that the production of antheridia is clearly preceded by a division of outer cortical cells, the outermost layer thus becoming the antheridial mother-cells. In the upper regions of the thallus a comparison of a sterile and a fertile area shows that in the former, if young, the outer layer of cortical cells is missing, but is developed in the soral area, forming the mother-cells. These, then, are not simply cells which would in any case be present, but they are specially developed on the antheridial plants to assist in the production of antheridia. These mother-cells are uninucleate and are only poorly pigmented.

The antheridia develop as protuberances of the mother-cell and are enclosed in the gelatinous wall of the latter, being cut off obliquely by the ingrowth of this wall (fig. 34 *b*). Dunn describes two spermatia as being detached in this way, but a surface view of the thallus (fig. 34 *a*) clearly shows that in several cases three are developed in succession from the flattened surface of the mother-cell. It is easy to overlook this if sections only are studied, since the antheridia are so crowded that it is difficult to ascertain how many are attached to each mother-cell. The antheridia stretch upwards to the surface of the "cuticle" which covers the thallus; the protoplasmic contents surrounding the nucleus round off, becoming nearly spherical (fig. 34 *b*). At this stage it is possible to see quite clearly the colourless antheridial wall surrounding the spermatium; this wall shows a distinct outer layer, especially at the apex and a swollen middle layer, while there is a definite inner refractive region around the central body (fig. 34 *b*). The spermatium escapes, enclosed in what appears to be a delicate wall, leaving behind the empty antheridial wall attached to the mother-cell (fig. 34 *b*). The observations of Dunn are, however, directly opposed to these results; she states and illustrates by figures that "no empty cell walls were seen attached to the spermatium mother-cell," and "the wall of the spermatium is a portion of the mother-cell . . . . no body is formed which would be homologous to the spermatangium of *Delesseria*." These statements, implying that the whole antheridium is cut off and liberated at maturity, can only be explained on the supposition that Dunn worked with microtomed sections or with material which had been much shrunken and in which the gelatinous walls would be far from easy to see.

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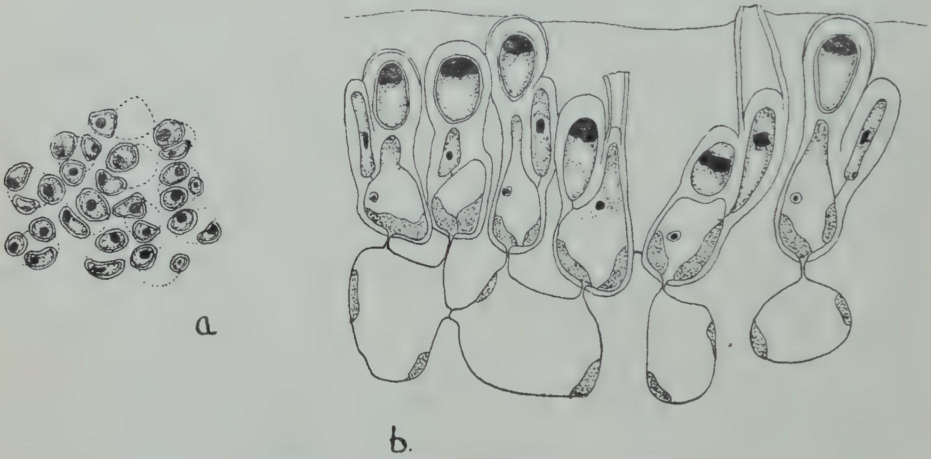
* The presence of antheridia was mentioned by Thuret (1855), and they have been described by Dunn (1917, p. 437) and Rosenvinge (1917, p. 155).

FIG. 34.



Antheridia in *Dumontia filiformis.* × 1800.

*a*. Surface view of part of a fertile area of an antheridial plant, showing the antheridia borne upon the flattened apex of the mother-cell (dotted).

*b*. Transverse section through a similar sorus. Both primary and secondary antheridia can be seen in optical sections in course of development.

Secondary antheridia are clearly developed within the empty walls of the primary ones; these new ones in many cases arise before the extrusion of the primary spermatia (fig. 34 *b*). In no case have tertiary antheridia been observed. The cytology of this form has not here been investigated, since it was clearly shown by Dunn that the nuclei behave in a similar way to that which has been described in this paper for the antheridial nuclei in many members of the higher Florideæ.

The development of the antheridia in *Dumontia filiformis*, together with the production and liberation of the spermatia, does not therefore appear to deviate in any outstanding particular from the course of events previously described for other species.

### (15) FURCELLARIA FASTIGIATA * Lam.

Material was obtained from Swanage, Shanklin, and Plymouth in January, February, and April respectively.

The antheridial plants of *Furcellaria fastigiata* have been known for many years, and before their function was recognized were classified as a peculiar variety of the normal plant characterized by the "little ovate-lanceolate, transparent, very pale, soft terminations of the branches" (Greville, 1830, p. 67). Dawson Turner, however, though not understanding the method of reproduction of the alga, attaches the following shrewd observation to his description of this variety :—"That these ovate transparent tips are in reality connected with the fructification I cannot allow myself to doubt, as well as from their peculiar form and substance, as from their appearing only at the time of the cylindrical pods, and, like them, withering and falling off, leaving the frond truncated. At the same time, when cut through, they exhibit no appearance of seed or granules, but are full of a transparent mucus, interwoven with reticulate threads in cylindrical meshes." Greville was under the impression that they were to be regarded as "imperfectly developed pods," while Thuret was the first to recognize their true significance. Sixty years later Rosenvinge made a slight investigation of Danish material, leaving, however, many points undetermined.

Antheridial plants are developed apparently in the spring (December to May in Denmark), and entirely resemble the vegetative plants except in the upper regions, where all the branches are terminated by much swollen, oval, nearly colourless "pods," varying in length, but in a healthy plant attaining to as much as 2 cms. These bodies are generally pale yellow or pink and somewhat hyaline, their characteristic transparent look and slimy feeling being due to the thick gelatinous "cuticle" enclosing the antheridia which are found in large numbers over the whole surface.

The "pods" though all performing the same function appear to be developed in two ways. In those found on young plants the normally dichotomously-formed apices of the thallus are replaced by pale-coloured tips, generally borne on a short stalk. On the other hand, in more complicated cases the apex dichotomises rapidly several times in succession, and the branches, lying close to one another, are each terminated by a "pod," giving a bushy appearance to the thallus. In either case, when ripe the "pods" shed their spermatia and then break away at the base, or in some instances, owing possibly to their succulent nature, are probably eaten away by animals which leave the truncated apices of the frond. From the latter, vegetative growth may take place in the normal way, continuing the growth of the thallus. Among drift material which has probably been thrown up from deeper water, plants have also been found in which no vegetative growth had taken place at the tips, but from the blunt end new "pods" were growing out in groups of three or four, each one being borne on a short stalk. This suggests that a single antheridial plant may bear at least two separate crops of antheridia; but whether this occurs successively in the same season or whether the two crops are separated by an interval of a year, could only be ascertained by careful observation of male plants throughout a year.

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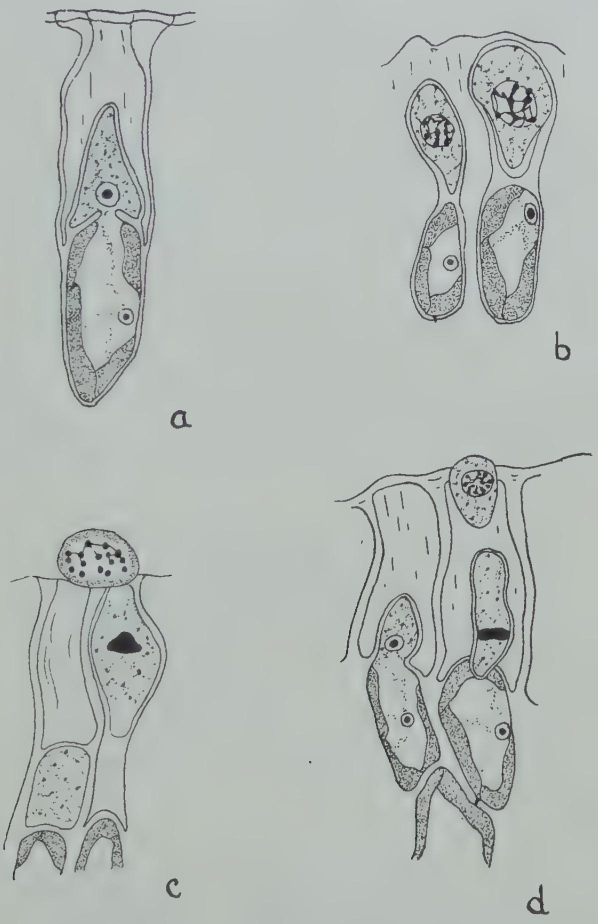
* Antheridial plants have been referred to by Dawson Turner (1808, p. 12), Greville (1830, p. 67), Thuret (1855), and Rosenvinge (1917, p. 167).

Before the formation of antheridia or the shedding of spermatia, these "pods" show a normal vegetative structure. When mature this consists of a central region of thin-walled hyphæ, surrounded by a zone of large colourless cells filled with dense contents, while without is a "cortex" of small pigmented uninucleate cells, enclosed in a common gelatinous "cuticle." The outer cells are seen to arise by one or more dichotomies of the cells immediately below them, so that the outer layer is in reality made up of pairs of cells, each pair arising from the cell directly beneath it (fig. 36 *a*); it is from this outer layer that the antheridial mother-cells develop. On their formation each outer cell elongates and becomes much swollen at the apex, appearing club-shaped (fig 36 *b*); plastids also which are pale in colour and have a bright refractive appearance accumulate in the enlarged tips. The cell is then divided by a cross wall, giving a lower cell normal in appearance and a short upper one, much swollen, pigmented and with a single nucleus (fig. 36 *c*). This upper one almost immediately divides by a longitudinal wall perpendicular to the periphery, giving two cells which, in an exact transverse section, appear to lie one above another. The cell which was therefore the outer one has now given three cells all joined by protoplasmic connections, a lower one subtending two upper ones which form the mother-cells (fig. 36 *d*). These latter have each a single nucleus and are pigmented, while the wall around them is somewhat swollen.

The antheridium arises as a sub-terminal conical projection from the mother-cell surrounded by the common gelatinous wall, pushing up through the now much swollen "cuticle" (fig. 36 *e*). At first this projection is pigmented, and it is not until the division of the mother-cell nucleus has taken place at the base of the young antheridium that the pigment disappears; no sign of definite plastids passing back into the mother-cell has been seen, but the pigment appears to degenerate, and it is noticeable that the protoplasm of the antheridium is markedly granular; possibly some of these conspicuous and highly refractive granules may be the products of degeneration of the plastids. The young, somewhat wedge-shaped antheridium with its single nucleus is abstricted by the ingrowth of the surrounding wall (fig. 36 *e*) and grows rapidly in length, always,

Fig. 35.



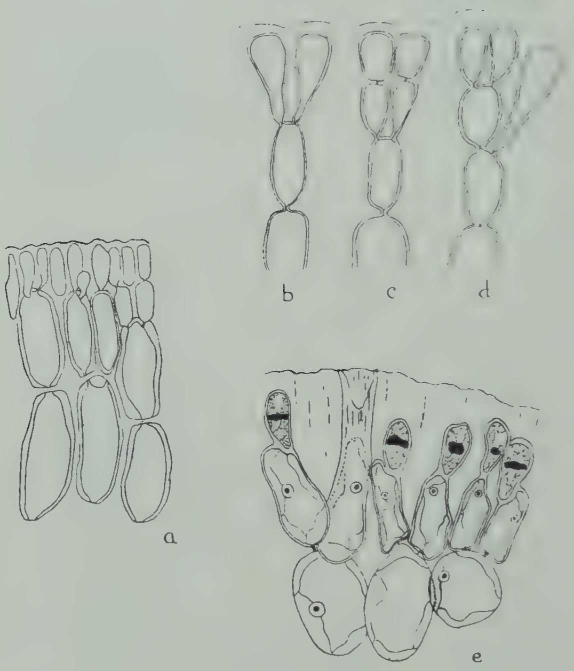
Stages in the formation of the antheridia of *Furcellaria fastigiata.* × 1800.

*a.* Young secondary antheridium being constricted off; nucleus in resting stage
*b.* Spermatium nearly ripe. Nucleus showing beaded deeply-staining reticulum.
*c.* Spermatium escaped. Chromatin granules clearly visible in the nucleus.
*d.* Right—formation of a secondary antheridium before the liberation of the first spermatium.

however, remaining long and narrow, possibly owing to the confined space. The antheridial wall stretches greatly until it reaches the surface of the "cuticle"; at this point it is ruptured (fig. 36 *e*), and the spermatium escapes through a circular aperture. The "cuticle" of a ripe "pod" seen in surface view from above is punctured all over with these ragged circular openings, through some of which spermatia can be seen escaping.

During the growth of this first primary antheridium, a second primary one has been forming in exactly the same way on the other side of the mother-cell. The expulsion of the spermatia from the antheridia is, however, slow, owing to the thickness of "cuticle" which has to be traversed; and while the upward growth of the primary antheridia is taking place, secondary ones are forming below each spermatium and have often been cut off before the latter has escaped (fig. 35 *d*). Generally, therefore,

FIG. 36.



*Furcellaria fastigiata.*

*a.* Outline drawing of a transverse section of the vegetative thallus, showing outer "cortex" of small cells developed from large storage cells below. × 750.

*b* to *d.* Stages in the development of antheridial mother-cells. × 1200.

*e.* Drawing of a transverse section of a "pod." The antheridial mother-cells are giving rise to primary antheridia. In one case the spermatium has escaped, leaving behind an empty sheath. × 1200.

two pairs of antheridia, one above the other, are developing at the same time from each mother-cell; the upper one of each pair is, of course, more mature. Everything points to the probability that even more antheridia are produced in the place of the empty ones, but they have not been seen. The proof should lie in the presence of the empty antheridial sheaths within one another, but owing to the close packing of the antheridia and the fact that the sheaths are only seen embedded in the "cuticle" and never free, there is difficulty in distinguishing the first-formed sheaths, and even more so, later-formed ones. The spermatia are on the whole large, within the antheridium measuring in some cases as much as $11 \times 5\,\mu$, though generally about $9{\cdot}5 \times 3{\cdot}5\,\mu$. On escape they become rounded off, and at that stage are clothed with a wall. It is impossible to say whether this wall has been developed before discharge; from analogy with the majority of other examined species one would expect this to be the case.

The single nucleus of the antheridial mother cell always remains small, but divides in a normal mitotic manner at the base of the antheridium, one of the daughter nuclei passing back into the mother-cell, and the other gradually increasing in size and moving into the young antheridium before the latter is abstricted. It then passes slowly to the centre of the spermatium, where it remains suspended by cytoplasmic threads, never appearing to take up the apical position so common in spermatia of other species. The details of nuclear structure show unusually interesting stages. Immediately after the antheridium is cut off, the nucleus can be seen lying near the point of constriction obviously in a resting condition, a structure similar to a nucleolus being distinctly visible and surrounded by a clear area in which indications of a faint network can be made out (fig. 35 *a*). At a somewhat later stage, when the spermatium is nearly ripe but has not yet ruptured the antheridial wall, the dark central body has entirely disappeared, and the nucleus consists of a deeply-staining reticulum with marked thickenings at the corners, the whole surrounded by a nuclear membrane (fig. 35 *b*). Finally, spermatia which have escaped show in their nuclei a number of well-defined, densely-staining granules or "Körnchen," as many as 16 or possibly more being present; linin threads connecting these together can be seen in some cases (fig. 35 *c*).

These stages, which can be repeatedly observed, clearly indicate, as suggested in the case of *Laurencia pinnatifida* (p. 205) and *Nitophyllum laceratum* (p. 199), that the nucleus of the antheridium when first formed passes definitely into a resting state; this, on the ripening of the spermatium, is followed by the early stages of a nuclear division which in the higher Florideæ is believed never to be completed. No evidence on the latter point is at present available for *Furcellaria*, for Rosenvinge (1917), who has studied the changes in the carpogonium, stated that he has never seen spermatia on the trichogyne; he considers that parthogenetic development takes place, sporogenous threads being formed apart from any fertilization stimulus. There are, however, no signs of degeneration in the spermatia, and it is difficult to believe that they should be produced in perfect condition and in such large numbers at the same season as the ripening of the trichogynes, if they are not called upon to take any part in the reproductive process.

## V. The Position of the Antheridial Organs.

The sexual plants of the Florideæ are usually diœcious, but the following members of the Nemalionales are reported as frequently exhibiting the monœcious habit: *Nemalion multifidum*, *Batrachospermum*, *Helminthora*, *Helminthocladia*, and *Bonnemaisonia asparagoides*. Antheridia and procarps borne on the same plant are also noted for some species of *Callithamnion* and for *Dudresnaya purpurifera*, *Glœosiphonia capillaris*, and *Halarachnion ligulatum*. It will be seen that this development is exceptional among the higher Florideæ.

The young antheridial plant is nearly always normal in appearance, resembling in every respect the young procarpial or tetrasporic thallus. Occasionally, however, as in *Martensia fragilis* or *Caloglossa Leprieurii*, it is smaller or has a more ephemeral existence than the female, and in *Dumontia filiformis* it is thought to die after discharging its spermatia (Dunn, 1917).

Thuret (1855) first pointed out that the antheridia are developed on these male plants in the same position as that in which the procarps and tetraspores are borne. This statement holds for the majority of cases, but in some species as *Laurencia pinnatifida* or *L. obtusa, Polyides rotundus,* etc., the antheridia resemble the procarps in position, differing in this respect from the asexual organs. In others, such as *Plocamium coccineum*, *Ceramium rubrum,* etc., the procarps occur in a different position from the antheridia and tetraspores, while in the species of *Polysiphonia* the position of the antheridia does not resemble that of either the tetraspores or the procarps.

The actual arrangement or grouping of the antheridia on the thallus is very varied. In *Nemalion* and *Batrachospermum* the antheridia are scattered indiscriminately upon the assimilating filaments, though in *Helminthora* and *Helminthocladia* the reproductive bodies are confined to clusters at the apex, while in *Liagora* and some members of the Lemaneaceæ special lateral antheridial branches are developed. Such clusters of branchlets are also borne laterally in *Callithamnion* (fig. 28), *Seirospora,* and *Halurus equisetifolius*, and terminally in *Spermothamnion* and *Ptilothamnion*, while in *Griffithsia corallina* they are arranged in definite whorls around the nodes (fig. 21). Finally, in such genera as *Sterrocladia, Galaxaura,* or *Laurencia,* these antheridial clusters are sunk in conceptacles on the surface of the thallus.

The more general position of the antheridia is, however, in superficial sori. These may be scattered without order as in *Rhodophyllis bifida* and *Cystoclonium* *purpurascens*, or the antheridia may be developed in acropetal succession, as in *Rhodymenia palmata* and *Chondrus crispus*. Among the Delesseriaceæ, transitions from sori developed on the thallus to those on special leaflets can be found, while in *Furcellaria fastigiata* the special structures take the form of a swollen apical "pod." In the Corallinaceæ, and probably also in the species of *Gracilaria*, the sori are sunk in conceptacles.

These various facts concerning the position of the antheridial groups can be summed up in the following scheme :—

1. Antheridia scattered, showing no regular order of development :— Nemalionales.
2. Antheridia combined in clusters on specially developed branchlets :—
    - (*a*) Single clusters .............................. *Callithamnion* spp. *Halurus equisetifolius.*
    - (*b*) Clusters aggregated in a definite order ........... *Griffithsia corallina.*
    - (*c*) Clusters sunk in conceptacles .................... *Laurencia* spp. *Galaxaura* spp.
3. Antheridia combined in a sorus :—
    - (*a*) Sorus on thallus showing no definite order of development. *Cystoclonium* spp. etc.
    - (*b*) Sorus on thallus showing definite order of development. *Rhodymenia palmata* etc.
    - (*c*) Sorus on a specially-developed organ ............. *Delesseria* spp. *Nitophyllum* spp.
    - (*d*) Sorus sunk in a conceptacle...................... Corallinaceæ.

## VI. The Position and Structure of the Antheridial Mother-cells.

Antheridia in the Florideæ are always developed from a cell which is variously known as the "cellule anthéridifère," the "Spermatangienmutterzelle," or the antheridial mother-cell. Schmitz (1883) stated that in all the Florideæ these mother-cells are the terminal and not the intercalary cells of branch systems. This is certainly the case in the vast majority of species, the mother-cells either forming an outer layer produced by division on the surface of a thallus as in *Nitophyllum* (pp. 195, 199), *Ceramium rubrum* (p. 229), *Furcellaria fastigiata* (p. 236), etc., or arising as the end cells of specially-developed branches which are not incorporated in the thallus tissue as in *Griffithsia corallina* (p. 215), *Callithamnion brachiatum* (p. 225), etc. Exceptions to this rule are, however, known in which both the intercalary and the terminal cells take part in antheridial production. Such cases are *Nemalion multifidum* (Cleland, 1919, p. 333), *Callithamnion roseum* (Guignard, 1889, p. 334), and *Halurus equisetifolius* (fig. 27). It seems probable that further investigation will bring to light more instances of this latter type of development.

In structure the antheridial mother-cell is unbranched, giving rise terminally, subterminally, or laterally to antheridia. Three species have been listed by Svedelius (1908) as bearing branched mother-cells : these are

*Choreocolax* Reinsch (*Harveyella* Schmitz), in which the mother-cell has now been shown by Sturch (1924) to be unbranched; *Champia parvula*, where the mother-cells certainly show no signs of branching on further investigation (see p. 193), and *Gigartina mamillosa.* The evidence for the latter case lies in a single figure given by Buffham (1896, fig. 8), the interpretation of which is somewhat doubtful.

Whatever the number of nuclei in the vegetative cells, the mother-cells are always uninucleate, the nucleus when not dividing lying near the base of the cell. The amount of pigment present varies considerably. In *Batrachospermum* and *Nemalion*, where the mother-cell is homologous with a vegetative cell, the pigment is found in both in equal quantities. The most common state of pigmentation is, however, the presence of reduced or rudimentary chromatophores, but in *Griffithsia Bornetiana*, *Kylinia rosulata*, and *Dumontia filiformis* the mother-cells are recorded as being usually completely colourless. In *Martensia*, where the chromatophores cannot be distinguished in the mother-cells, the suggestion is made by Svedelius (1908) that the dense protoplasm present is due to the solution of the plastids in the plasma for use as food material.

## VII. The Development of the Antheridia and Spermatia.

The antheridia (or spermatangia of German authors) are developed as terminal, subterminal, or lateral outgrowths from the upper (outer) surface of the antheridial mother-cells. There are, however, few records of terminal antheridia which can be regarded with any confidence. *Champia parvula* and *Cystoclonium purpurascens* have both been said to exhibit this characteristic, though this is now known not to be the case (see p. 192 and Kylin, 1922); *Hypnea musciformis* and *Pterocladia capillacea* have also been placed in this category (Guignard, 1889) together with *Peyssonellia squamaria* (Thuret, 1855), but on such slight evidence that re-examination with the aid of modern technique would probably lead to other conclusions. The terminal method of production is, however, both described and figured clearly by Svedelius (1908) for *Martensia fragilis*, by Guignard (1889) for *Melobesia membranacea*, and by Sturch (1924) for *Harveyella pachyderma*, though it must be noted with regard to the latter that in the closely-related species *H. mirabilis* "the antheridia are produced obliquely and laterally."

Antheridia are developed laterally in no particular order or number in *Batrachospermum* and *Nemalion*. Among the higher Florideæ, however, the development has become more regular, a definite number of primary antheridia being produced in a subterminal rather than lateral position, and ripening in orderly sequence around the upper surface of the mother-cell. The number appears to vary from two to four, only two being said to occur in *Delesseria sanguinea* (Svedelius, 1912), *Lemanea fluviatilis* (Kylin, 1922), *Chondrus crispus* (p. 187), *Furcellaria fastigiata* (p. 238), and *Rhodymenia* *palmata* (Delf and Grubb, 1924). Kylin (1922) lists eight species in which two *or* three antheridia are found, while three antheridia arising from a mother-cell are definitely known in a number of cases some of which are recorded in this paper (see p. 249). Four antheridia to a mother-cell is a rare occurrence only known with certainty in five instances—*Chondria tenuissima* and *Callithamnion roseum* (Guignard, 1889), *Laurencia pinnatifida* (p. 204), *Halurus equisetifolius* (p. 222), and *Polysiphonia violacea* (p. 213). It is noticeable that in those cases where the mother-cells are closely packed or confined by a thick "cuticle" the number of antheridia appears to be strictly limited by the available space.

The antheridia develop as protuberances of the wall and protoplast of the mother-cell, and into these slight projections passes the nucleus formed by the division of the mother-cell nucleus. As a rule the other contents of the antheridium are solely cytoplasmic, though the presence of chromatophores or portions of plastids has been recorded for *Nemalion multifidum* (Wolfe, 1904), *Batrachospermum* (Osterhout, 1900), and possibly these bodies also occur in *Furcellaria fastigiata* (p. 237).

The young antheridium is either long and narrow (fig. 9 *a*) or round and swollen (fig. 20 *b*). When it is equal in length to the mother-cell, the contents are abstricted from those below by a ring-like ingrowth of the surrounding elongated mother-cell wall, the constriction generally taking place at a level with the upper surface of the mother-cell, though in *Ceramium rubrum* it is above this level (p. 231). The fact that the spermatium is separated by abstriction and not by a normally-formed cross-wall does not appear to have been generally recognized; in the cases here described it seems impossible to doubt that the protoplasmic contents gradually become narrower at the point of separation until only a small connecting strand is left which presumably passes through a pit in the otherwise complete wall (fig. 12 *b*); finally, even this connection is no longer visible.

A rapid ripening of the antheridium now takes place; it generally swells, the cytoplasm becoming vacuolate and the nucleus taking up either an apical or central position. The wall thickens greatly, and in some cases can be seen to show three layers—a thicker outer one generally denser at the apex, a clear swollen central layer, and then around the contents which will form the spermatium a very narrow, highly refractive region (fig. 27 *b*). Ultimately a point is reached, at any rate in the great majority of cases, when a split occurs at the apex of the elastic surrounding wall, and through the narrow aperture thus formed the cytoplasm and nucleus slip out as a single spermatium. In those species where the antheridia are borne on filamentous branches (e. g. *Griffithsia*) the exit of the spermatium is quite simple, since it is not hampered by the surrounding "cuticle" of a thallus; in other cases (e. g. *Rhodymenia palmata*) the "cuticle" peels off in the region of an antheridial sorus. But in such species as *Chondrus crispus* or *Furcellaria fastigiata*, where the "cuticle" is very thick, the antheridial wall continues to elongate until it reaches the surface of the latter; then the wall splits and the spermatium escapes direct into the surrounding water (fig. 36 *e*). In *Callithamnion roseum* (Guignard, 1889) little caps are said to be formed at the apex of the antheridia, liberating the spermatia, and in *Harveyella* "usually the outer coat (*i.e.*, 'cuticle') is so weakened by the mass of spermatia that it flies off like a broken spring and all the spermatia are set free at once" (Sturch, 1924).

Species have been described in which the whole antheridium is apparently cut off and liberated at this point, the two best-known records being those for *Polysiphonia violacea* (Yamanouchi, 1906) and *Dumontia filiformis* (Dunn, 1917). Figures and observations given in this paper have, however, clearly shown that in both these species the antheridial walls remain behind after the spermatia have passed from them (figs. 20 *c* and 34 *b*). Though denied by Lewis (1909) re-examination would probably show that this same behaviour takes place in *Griffithsia Bornetiana* in view of the fact that in two nearly-related species (*G. corallina* and *Halurus equisetifolius*) walls can clearly be made out (figs. 24 and 27). In the case of *Martensia*, although Svedelius believes that the whole or part of the antheridial wall is cut off with the spermatium, yet he clearly figures mother-cells with empty gelatinous sheaths standing up above them (1908, pl. 4. fig. 6).

The spermatium, immediately on discharge, is oval in form and may be as long as 11 $\mu$ (*Furcellaria*); it rapidly, however, becomes rounded off, measuring in diameter anything from 2 or 3 $\mu$ (*Callithamnion*, *Griffithsia*) to 6 or 7 $\mu$. At this stage it consists of delicate cytoplasmic contents surrounding a central nucleus, but opinions differ as to whether or not it is enclosed in a wall. Svedelius (1912) reported that in *Delesseria sanguinea* the spermatium is discharged as a naked protoplast, while Kylin, after examining this latter species together with *Rhodomela virgata* (1914) and *Bonnemaisonia asparagoides* (1916), agreed with this, stating, however, that sooner or later a wall is acquired. Guignard (1889), on the other hand, observed walls around all the escaping spermatia he examined, and Yamanouchi believes that in *Corallina officinalis* the spermatium "has a thin wall derived entirely from the mother-cell" (1921, p. 93). In all the species described in this paper the spermatium when liberated appears to be clothed with a very delicate, highly refractive wall. This, in some cases at least, seems to be present when the body is still within the antheridium (*Polysiphonia fastigiata*, fig. 18 *b* & *c*, *Laurencia pinnatifida*, fig. 14, etc.), for, as the spermatium approaches maturity, a narrow layer appears around the body, staining less deeply than the true surrounding antheridial wall. This internal wall can be seen even more distinctly when the spermatium has contracted away from the base of the antheridium, or when half in and half out of the latter (fig. 18 *c*), but whether it is an inner layer of the antheridial wall or an entirely new structure is not clear.

Secondary antheridia are known to occur in several species, but their presence has often been overlooked. Guignard figured them for *Griffithsia corallina* and *Chondria tenuissima* (1889, pl. 6. figs. 6, 7), and Zerlang (1889) described them for *Wrangelia penicillata*. Svedelius notes them for *Martensia fragilis* (1908), though he fails to find any development comparable to this in *Delesseria sanguinea* (1912), except in very rare cases; it, however, occurs regularly in *Scinaia furcellata* (1915). Rosenvinge notes the phenomenon in *Dumontia incrassata* (1917, p. 157), but Dunn (1917), working on microtomed sections of this species, failed to see it. Kylin neither denies nor describes the occurrence of these secondary antheridia in the many species which he has investigated, apparently not having observed them. In every species described here bearing mature spermatia, with the exception of *Polysiphonia* spp., it has been possible to find secondary antheridia developing and forcing their way up through the empty primary ones (cp. fig. 27).

In some instances a third series is formed (*Callithamnion brachiatum*, fig. 30), while in *Nemalion lubricum*, Kurssanow (1909) figured as many as six antheridial sheaths one within another arising from the same point. The apparently multiple formation in *Harveyella pachyderma* (Sturch, 1924) and *Melobesia* (Guignard, 1889) seems to require further investigation.

The fate of the mother-cells following on the cessation of the production of antheridia is various. In some cases (*Martensia*, *Delesseria*) the leaflets on which they were borne die away, or the part of the thallus disappears (*Furcellaria*). In other species the mother-cells simply return to the function of normal vegetative cells, and it is no longer possible to distinguish that they have played any distinctive part in the life-history (*Chondrus crispus*, *Rhodymenia palmata*).

## VIII. The Cytology of Spermatial Development.

Spermatial development seems to include a characteristic and, on the whole, uniform series of nuclear changes, both in the mother-cell and in the antheridium. The single nucleus of the mother-cell, which is generally at the base of the cell, appears, in the resting condition, to consist of two regions—a central denser one and a colourless outer area. According to the figures given by Kylin and Yamanouchi, this appearance is explained in *Griffithsia corallina*, *Rhodomela virgata*, and *Polysiphonia violacea* by the central position of the spherical nucleolus, the surrounding area being occupied by a delicate network bearing chromatin granules. On the first signs of the formation of a spermatium this nucleus passes up to the base of the small projection, there entering into an early prophase (cp. Kylin, 1914, fig. 14); here it undergoes the normal karyokinetic division similar to that of vegetative nuclei; the mitotic figures are exceedingly small, and it is generally impossible at this stage to count the chromosomes, since they appear only as a dark line along the equator or as a densely-staining mass at either pole. Of the two daughter nuclei thus formed, one enters into the young antheridium, while the other returns to the base of the mother-cell, and remains there in a resting condition until the formation of a further antheridium. This mother-cell nucleus may repeat the process as many as eight times in the case of those species in which four primary and four secondary antheridia are formed from each mother-cell.

The antheridial nucleus passes up the length of the antheridium, until, when this is mature, the nucleus is to be found as a large somewhat elongated body 2 to 3·5 $\mu$ in diameter, occupying either a central or an apical position (*Furcellaria* and *Laurencia* respectively). Opinions differ as to the behaviour of the nucleus when first formed; Yamanouchi states that in *Polysiphonia violacea* "the chromosomes maintain their individuality and are united by linin threads" (1906, p. 11), while Svedelius thinks that the same may hold good for *Martensia fragilis* (1908) and *Delesseria sanguinea* (1912), thus implying that this nucleus never passes through a resting stage before entering into the next division. On the other hand, Kylin has shown in two cases that in the young spermatium the nucleus can be seen in the resting condition, later passing into prophase (*Bonnemaisonia asparagoides*, 1916, and *Rhodomela virgata*, 1914). This has also been observed in this paper in cases where it has been possible to make out detailed structure, and particularly in *Furcellaria fastigiata* (fig. 35), *Laurencia pinnatifida* (fig. 14), and *Nitophyllum laceratum* (fig. 12).

In these latter species the antheridial nucleus after its formation is first seen as a dark central region surrounded by a paler area; in *Delesseria sanguinea* Kylin (1922) attempted to show that there was a small central nucleolus, though this was absent in the closely-related *D. sinuosa* and *D. ruscifolia*; in *Rhodomela virgata* (1914) it was absent or could only be made out with difficulty, while it has not been seen in any of the forms examined here. But what appears to be the dark nucleolus is apparently a dense mass of chromatin or possibly very minute chromatin granules staining deeply and connected by linin threads with one another; a similar construction of the pseudo-nucleolus has been shown by van Wisselingh to be present in *Spirogyra*. Sooner or later changes take place in the nucleus, while the spermatium is still retained within the antheridium. The definite nuclear membrane is lost, and there appears a well-defined and regular number of small deeply-staining bodies known as Körnchen, Karyosomes, or granules, united to one another by delicate linin threads. It seems probable that these Körnchen represent and indeed may be true chromosomes. In every case where detailed examination of the spermatial nucleus has been undertaken it is recorded as being in this condition of prophase at the time of discharge of the spermatium, about twenty such instances being known in addition to those recorded in this paper.

The subsequent fate of the spermatial nucleus appears to vary. In *Batrachospermum* (Schmidle, 1899; Kylin, 1917) and *Nemalion* (Wolfe, 1904; Kylin, 1916; Cleland, 1919) it is said to divide and give two daughter nuclei when the spermatium becomes attached to the trichogyne. In other genera, however, this division is not known to take place, but the spermatial nucleus while still in prophase passes down the trichogyne and fuses with the carpogonial nucleus. There appears, therefore, to be a marked difference in this respect between the lower and the higher Florideæ, the evidence from the former pointing to the probability that what is now a single spermatium originally possessed the potentiality of becoming two. In the higher Florideæ, even this nuclear division within the spermatium has become suppressed, the only remaining sign that it ever occurred being the condition of prophase in which the nucleus is found at the time of fertilization.

Although it is almost impossible to obtain an accurate chromosome count in the mitotic figure in the antheridial mother-cell, this has been done in the antheridium in twenty-one species besides those recorded in this paper by counting the number of granules at the time of prophase. Owing to the small size of the nuclei, the numbers are not to be regarded as equally accurate with those counts made in the comparatively large vegetative or tetrasporic nuclei, and indeed in such cases as *Nemalion multifidum*, where a count has been taken by two different workers, there is often a divergence of opinion (Kylin, 1916; Cleland, 1919). It is curious to note that Kylin finds ten chromosomes to be the haploid number in both *Batrachospermum* and *Nemalion* representing the lower Florideæ, while in the eleven species of the higher Florideæ where he has counted the number he always obtains twenty or about twenty. This uniformity is not borne out by other workers, Lewis (1919) recording seven for *Griffithsia Bornetiana*, Dunn (1917) seven for *Dumontia filiformis*, and Yamanouchi (1921) twenty-four for *Corallina officinalis*. The same variability has been found in the different species investigated here, the numbers varying from about eight in *Nitophyllum laceratum* and *Ceramium rubrum* to sixteen or possibly more in *Furcellaria fastigiata*.

## IX. The Homologies of the Antheridia.

The antheridia of the Florideæ can be compared with similar structures in three different groups. Among the algæ the only close resemblance is to be found in the Chlorophyceæ, the similarity with *Coleochate* in methods of sexual reproduction having long been recognized. The antheridia in this genus arise in a manner and position almost exactly comparable to that in the Nemalionales, the contents of an antheridium in *C. scutata* consisting of a nucleus, cytoplasm, and plastids. At this point the comparison breaks down, for the liberated spermatozoid is said to be both ciliated and naked.

Even if, however, no close phylogenetic link exists between *Coleochæte* and the Florideæ, there is here an interesting example of parallel evolution in the male as well as in the female reproductive organs.

The resemblance between the Florideæ and certain groups of the Fungi has been noted by several writers, notably Sachs (1882), Schmitz (1883–93), and Dodge (1914). These parallels have mainly been drawn from comparisons between the ascogonium and the carpogonium of the Ascomycetes. Structures known as antheridia are, however, found in many species of the latter group, and particularly in some of the Pyrenomycetes, where these bodies are borne at the extremities of very fine uninucleate hyphæ gathered into spermogonia. In *Gnomonia erythrostoma* the resemblance to the Florideæ is very close, for the antheridia are said to be constricted off terminally, each containing "a long thread-like nucleus and a relatively small amount of cytoplasm" (Brooks, 1910). Similarly, in *Gymnosporangium clavariæforme* (Blackman, 1904) figures show that the spermatia are cut off from the hyphæ by the ingrowth of the surrounding wall, the walled spermatium containing a fine granular cytoplasm and a single nucleus. Characters such as these in antheridial structure suggest that there may be something more here than an accidental resemblance to the antheridia of the Florideæ.

The spermatia of the Laboulbeniales offer possibly an even closer comparison. Within this group they are developed in two ways: exogenous spermatia are cut off as uninucleate rod-shaped bodies from a specialized branch, and there is evidence that "as soon as they drop off they are replaced by others from the same base" (Faull, 1911, p. 650); endogenous spermatia are constricted off one after another from a mother-cell, and covered by a thin protoplasmic membrane, are extruded through a more or less elongated flask-shaped neck (Thaxter, 1908). In other words, they escape as thin-walled bodies through a split in the antheridial wall, in a manner entirely comparable to that described here for Florideæ. The resemblances are so close that one can imagine that the ancestors of the Laboulbeniales may have been minute Florideæ which first became parasitic upon aquatic insects and thus reduced in size, only later migrating to an existence upon aerial hosts. Such comparisons as the above, however, throw little light upon the origin of the antheridial complex, and only tend to emphasize the highly-developed character of the male organs in the Florideæ.

## X. Classification of the Florideæ on the Basis of Spermatial Types.

The only published classification of the Florideæ based on the methods of spermatial production is that of Svedelius (1908). The species were subdivided on two criteria dealing with the structure of the antheridial mother-cell: first, whether this resembled or differed from a vegetative cell and, second, whether it was simple or branched. This second character has been rejected in the following scheme, and in its place the variations in the position and number of the antheridia have been substituted. Only three species have been included in the group with terminal antheridia, and when further knowledge is available it seems probable that this sub-group will not persist.

## Classification of Spermatial Types.

A. Antheridial mother-cell not differing from a vegetative cell either in form or contents.

*Nemalion* spp. (Wolfe, 1904).
*Batrachospermum* spp. (Kylin, 1916).

B. Antheridial mother-cell differentiated from a vegetative cell.

1. Antheridia developed terminally on the mother-cell.

*Martensia* spp. (Svedelius, 1908).
*Melobesia* spp. (Guignard, 1889).
*Harveyella pachyderma* Batt. (Sturch, 1924).

2. Antheridia developed sub-terminally on the mother-cell.

(*a*) Mother-cell subtending two primary sub-terminal antheridia.

*Delesseria sanguinea* Lamour. (Svedelius, 1912).
*Rhodymenia palmata* Ag. (Delf & Grubb, 1924).
*Chondrus crispus* Stackh. (p. 184).
*Furcellaria fastigiata* Lam. (p. 238).
*Lemanea fluviatilis* Ag. (Kylin, 1922).
*Laurencia obtusa* Lam. (p. 207).

(*b*) Mother-cell subtending two *or* three primary sub-terminal antheridia.

*Scinaia furcellata* Bivona (Svedelius, 1915).
*Cystoclonium purpurascens* Kütz. (Kylin, 1922).
*Delesseria sinuosa* Lam. (Kylin, 1922).
*D. ruscifolia* Lam. (Kylin, 1922).
*D. alata* Lam. (Kylin, 1922).
*Lomentaria clavellosa* Gaill. (Kylin, 1922).
*Plocamium coccineum* Lyngb. (Kylin, 1922).
*Polysiphonia nigrescens* Grev. (Kylin, 1922).
*Rhodophyllis bifida* Kütz. (Kylin, 1922).

(*c*) Mother-cell subtending three primary, sub-terminal antheridia.
*Bonnemaisonia asparagoides* Ag. (Kylin, 1916).
*Polyides rotundus* Grev. (Kylin, 1922).
*Ceramium rubrum* Ag. (p. 231).
*Griffithsia corallina* Ag. (p. 218).
*G. Bornetiana* Farlow (Lewis, 1909).
*Nitophyllum Hilliæ* Grev. (p. 196).
*N. laceratum* Grev. (p. 199).
*Lomentaria ovalis* Endl. (p. 189).
*Champia parvula* Harv. (p. 193).
*Dumontia filiformis* Grev. (p. 234).
*Callithamnion brachiatum* Bonnem. (p. 223),
*Rhodomela virgata* Kjellm. (Kylin, 1914).
*Polysiphonia fastigiata* Grev. (p. 210).

(*d*) Mother-cell subtending four primary sub-terminal antheridia.
*Polysiphonia violacea* Grev. (p. 213).
*Chondria tenuissima* Ag. (Guignard, 1889).
*Laurencia pinnatifida* Lam. (p. 204).
*Callithamnion roseum* Harv. (Guignard, 1889).
*Halurus equisetifolius* Kütz. (p. 222).

It is clear that the position of the antheridia and also their number varies greatly even among genera of the Florideæ, which on anatomical and other grounds are regarded as closely related. Yet any intensive study of the male organs in this group cannot fail to impress the inquirer with a sense of the remarkable uniformity exhibited in the details of development and liberation in every case. Although the examples selected for examination in this paper are drawn from species which in outward form and cystocarpic development differ widely, yet in each case the formation, abstriction, and liberation of the contents of the individual antheridium is the same. Similarly, no deviation has been observed so far from what has come to be regarded as the normal cytological behaviour in the antheridium. Thus the course of events in the development of these male organs points undoubtedly to the fundamental resemblance underlying the species of the higher Florideæ and their probable common origin.

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## SUMMARY.

1. A detailed investigation of the antheridia in fifteen species of the Florideæ has been undertaken with a view to ascertaining the course of events in the development and liberation of the spermatia. Of the species examined, the antheridial plants were previously entirely unknown in one case (*Nitophyllum laceratum*); in ten instances (*Chondrus crispus, Lomentaria ovalis, Champia parvula, Nitophyllum Hilliæ, Laurencia obtusa, Polysiphonia fastigiata, Halurus equisetifolius, Callithamnion brachiatum, Ceramium rubrum*, and *Furcellaria fastigiata*) little or nothing was known beyond the existence of male plants, and only in four species (*Laurencia pinnatifida, Polysiphonia violacea, Griffithsia corallina*, and *Dumontia filiformis*) had more or less complete examinations of the structure been made.

2. It has been shown that in each case a definite number of antheridia are produced sub-terminally from an antheridial mother-cell which is specially developed for this function at the apex of a branch or upon the surface of the thallus. The number of primary antheridia from each mother-cell may be two, and is commonly three, even four or rarely five being found. These antheridia invariably arise as colourless protoplasmic uninucleate outgrowths clothed in the elongated gelatinous wall of the mother-cell. By the ring-like ingrowths of this wall at the base, the contents are abstricted and form the single spermatium.

3. The mature antheridium has been shown to consist of a swollen gelatinous wall surrounding a single apical nucleus, a central vacuole, and a small amount of cytoplasm. The wall is three-layered; the outermost layer is narrow and deeply staining; within is a gelatinous region which swells greatly at the time of liberation of the spermatium, while around this body is a narrow highly refractive region which may possibly represent the spermatial wall. The spermatium when free measures from 4 to 9 $\mu$ in diameter, and in some instances is undoubtedly surrounded by a very delicate wall.

4. The method of liberation of the spermatium has been studied from unshrunken material, and in *Laurencia* and *Ceramium* has actually been watched in living material. The exit always takes place by means of a split in the antheridial wall beginning in the swollen apical region and sometimes extending to the base (i. e. *Laurencia*). Through this narrow aperture the whole contents escape, leaving behind them the empty antheridium as a shrunken gelatinous sheath. In some species, e. g. *Rhodymenia palmata*, the "cuticle" extending over the thallus is known to peel off in the region of a ripe antheridial sorus, leaving the antheridia freely exposed to the surrounding medium. It has also been demonstrated here, that in other species, e. g. *Chondrus, Furcellaria, Ceramium*, and *Polysiphonia*, this does not occur, but the developing antheridia grow up *through the cuticle until they reach*

the surface, where they discharge their spermatia. In no case is the complete antheridium cut off and liberated as described by Yamanouchi for *Polysiphonia violacea* or Dunn for *Dumontia filiformis*.

5. With the exception of the species of *Polysiphonia*, observations made on mature plants have shown that secondary antheridia develop within the shrivelled sheath-like remains of the primary ones, discharging their contents in a similar way. In one species (*Callithamnion brachiatum*) tertiary antheridia were found.

6. Cytological investigation shows that the antheridial mother-cell is always uninucleate. This nucleus divides at the base of each young antheridium, and the daughter nucleus passes into the upgrowing projection. At this stage it is in the resting condition, but as it moves to the apex of the antheridium it passes into early prophase, deeply-staining granules becoming visible, connected with one another by linin threads. When the spermatium escapes, the nucleus consists of a definite number of chromatin granules or Körnchen united by linin threads. This number never varies within a species, and it is probable that these granules are the true chromosomes.

7. A classification of the spermatial types among the Florideæ has been drawn up, based on the position of the antheridial mother-cells and the number of primary antheridia. From this and the preceding investigation it can be seen that while the methods of spermatial production are of little use as a character of systematic importance, yet the fundamental similarity underlying the development in all species points to a common origin for all types.

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# A Third Contribution to the Composite Flora of Africa. (*Continued from* vol. xxxvii. (1906) pp. 298–329.) By S. Moore, B.Sc., F.L.S.

[Read 7th May, 1925.]

The bulk of the specimens proposed as types of new species appearing in this memoir belong to the Gossweiler and Kassner collections, made, the former chiefly in Angola, the latter in N. and N.W. Rhodesia and the eastern end of the Belgian Congo and immediately neighbouring districts. Both these collections are full of novelties, of which some have been described in this country and on the Continent; but a large number still await description at the hands of those in a position to undertake the task. Besides these a few types are due to other collectors, viz.: Dr. Burtt Davy (Belgian Congo), Miss Henderson (British Central Africa), Mr. F. Eyles (Rhodesia), Mrs. Jelf (N.E. Rhodesia), Mr. Swynnerton (Tanganyika Territory), Rev. E. H. Clark (N.E. Rhodesia), and Dr. Bagshawe (Uganda). The Dümmer (Uganda) and Mr. John Buchanan (Nyassaland) collections have also been laid under contribution. The types are in the British Museum.

## GUTENBERGIA.

Gutenbergia Gossweileri, sp. nov. *Herba* erecta, fere a basi ramosa; *ramis* tetragonis sparsim sericeo-pubescentibus; *foliis* inferioribus oppositis superioribus alternis sessilibus oblongis obtusis basi haud nisi brevissime amplexicaulibus supra leviter scabriusculis in sicco fuscis subtus albo-tomentosis; *capitulis* parvis anguste campanulatis 4–6-flosculosis in cymas laxas ramos terminantes folia longe excedentes dispositis; *involucri* sparsim sericei phyllis 3-serialibus lanceolatis acuminatis margine anguste membranaceis; *corollis* dilutissime cœruleis brevibus inclusis sparsim sericeis tubo infundibulari quam lobi triangulares longiore; *achæniis* late turbinatis obscure costatis breviter setulosis brunneis.

Angola, Casuango, Kuiriri; *Gossweiler*, 2741.

Planta bispithamea. Folia summa 5 cm. × 8 mm., pleraque ± 3 cm. × 4 mm., summa ± 2 × 3 mm. Cymæ sæpe circa 6 × 6 cm. Pedunculi proprii graciles, ± 4 mm. long. Capitula pansa 4 × 2·5 mm. Involucri phylla extima 2 mm., intermedia 3 mm., intima 4 mm. long. Corollæ ægre 2 mm. long.; lobi ·35 mm. Achænia 1 mm. long.

A taller stronger-growing plant than *G. polycephala* Oliver & Hiern, with many more and smaller heads, short "whitish-blue" corollas, and different achenes.

Gutenbergia tenuis, sp. nov. *Herbacea*; *caule* tenero subdistanter folioso sericeo-pubescente; *foliis* oppositis (summis vero alternis) sessilibus oblongis acutis vel acutiusculis supra leviter scabriusculis subtus subtiliter albo-sericeo-tomentosis; *capitulis* parvis campanulatis 6-flosculosis in cymam sublaxam oligocephalam sericeam folia summa facile excedentem digestis; *involucri* sericei phyllis 3-serialibus oblongo-lanceolatis breviter acuminatis pallidis margine membranaceis additis perpaucis extimis brevissimis ovatis acutis; *corollis* purpureis breviter exsertis tubo anguste infundibulari extus sparsim sericeo lobis oblongis obtusis tubo brevioribus; *achæniis* compressis ambitu suborbicularibus obscure 5 (?)-costatis sparsim brunneo-sericeis.

British Central Africa, Nyika Plateau; *Miss Henderson.*

Folia 2 × ·5 cm., summa 10–13 × 3·5–4 mm., supra in sicco pallide viridia. Cyma 3 × 2 cm. Pedunculi proprii tenues, 2–5 mm. long. Capitula (flosculis inclusis) 5 × 4 mm. Involucri phylla extima 1 mm. long., exteriora 2 mm. interiora 3–4 mm. long. Corollæ 4 mm. long., harum lobi 1 mm. Achænia 1 mm. long.

## GOSSWEILERA.

Gossweilera paludosa, sp. nov. *Herbacea*, erecta; *caule* sat robusto hac atque illac ramulos breves tenues emittente crebro folioso costato pubescente; *foliis* alternis sessilibus lineari-lanceolatis acute mucronulatis basi angustatis integris pag. utraque scabris; *capitulis* pro genere majusculis ∞-flosculosis corymbum terminalem folia longe superantem crebro bracteatum pubescentem efficientibus vel ramulos solitatim vel 2–3-natim terminantibus; *involucri* subhemisphærici 5-serialis pubescentis phyllis oblongis apice discolori acuminatis interioribus appendice parva erosa onustis; *receptaculi* convexi alveolati paleis involucri phyllis similibus nisi angustioribus; *corollis* exsertis; *achæniis* oblongis parum curvatis tetragonis obscure costatis glabris politis dilute brunneis quam pappus multo longioribus.

Angola, Cuanza, in wet situations along watercourses between Quitomba and Camabatela; *Gossweiler*, 7402.

Folia pleraque 3–5 cm. × 4–8 mm., in sicco viridia, subtus pallidiora. Inflorescentia circa 14 × 12 cm.; hujus bracteæ foliis similes sed minores. Involucra 8 × 11 mm.; phylla ext. 4·5–5 mm., int. 6 mm. long. Corollæ purpureæ, 6·5 mm. long.; tubus infundibularis 4 mm. long.; lobi lineari-lanceolati acuti tubum semiæquantes. Stylus crassiusculus; rami teretes, hispiduli, 2 mm. long. Achænia longit. 2 mm. leviter excedentia; pappus ·5 mm. alt.

Differs from *G. lanceolata*, the only other species (see Journ. Bot. xlvi. (1908) p. 291), in foliage and larger heads, among other features.

The most distinctive feature about this genus is its possession of large receptacular paleæ, a very rare occurrence in *Vernonicæ*: in this it resembles O. Hoffmann's *Dewildemania*, a native of the Congo Free State, which, however, instead of a cupular pappus, has one composed of two rows of scales. These paleæ probably serve to protect the florets against the attacks of insects.

Muschleria Stolzii, sp. nov. *Herbacea*; *caule* erecto pauciramoso tetragono optime costato scabriusculo; *foliis* radicalibus caulinisque sessilibus lineari-oblanceolatis obtusis basi obtusis margine dentatis vel denticulatis sed sæpe integris membranaceis utrinque scabriusculis vel fere omnino glabris; *capitulis* circa 30-flosculosis in corymbum terminalem laxum oligocephalum scabriusculum ordinatis nonnunquam fere solitariis; *involucri* anguste campanulati phyllis circa 6-serialibus lineari-lanceolatis acuminatis saltem in sicco fuscis; *corollis* exsertis; *achæniis* oblongis 5-costatis glabris; *pappo* brevi cupulari ore erosulo additis setis interioribus paucis (interdum usque 10) breviter barbellatis.

Tanganyika Territory, Kyimbila District; *A. Stolz*, 2595.

Planta bispithamea. Folia summum 8 × 15 cm., sæpius ± 5 × 1 cm., in sicco viridia. Inflorescentiæ 10–15 × 7–9 cm.; harum bracteæ oblongæ, obtusæ, ± 1 cm. long. Capitula pansa 7 × 6 mm. Involucri phylla circa 5 mm. long., extima paullulum breviora. Corolla 5 mm. long.; tubus anguste infundibularis; lobi oblongo-lanceolati, 2 mm. long. Achænia fere 1·5 mm. long., pallida. Pappi cupula ·4 mm. alt.; hujus setæ 1 mm. long.

Since its establishment ten years ago (Journ. Bot. lii. (1914) p. 89) this genus has remained monotypic. The plant just described differs from the typical species in habit and in the presence of setæ within the pappus cupule, and may therefore perhaps be rightly considered the type of a new genus. But considering the multiplication of small genera in the immediate neighbourhood of *Muschleria*, it would seem better to enlarge slightly the conception of the genus, as is done here.

## ERLANGEA.

Erlangea (§ *Bothriocline*) sengensis, sp. nov. *Herba* erecta verisimiliter eramosa fere trispithamea; *caule* fere omnimodo folioso tetragono optime striato pubescente dein glabrescente; *foliis* oppositis (perpaucis summis alternis) sessilibus ovato- vel lanceolato-oblongis obtusis basi rotundatis vel obscure cordulatis supra scabridis fuscisque subtus dilute griseo-tomentosis; *capitulis* pro genere majusculis solitariis a foliis ultimis diminutis involucratis; *involucri* subhæmisphærici phyllis 6-serialibus ovatis apice mucronatis dense griseo-tomentosis intimis oblongis acutis inferne glabris superne griseo-pulverulentis; *achæniis* sursum turbinatis angulatisque deorsum angustatis minutissime puberulis; *pappi* setis perpaucis verisimiliter sæpe unicis ciliato-barbellatis caducissimis.

Belgian Congo, slopes of Mt. Senga; *Kassner*, 2096.

Folia pleraque 7–8 × 2·5–3 cm.; summa gradatim minora, ultima modo 1·5 cm. long. Involucra 16 × 14 mm.; phylla extima 10 mm., interiora 12–13 mm. long. Corolla nondum pansa 10 mm. long. Achæniæ pars sup. ·75 mm., pars inf. 1·75 mm. long. Pappi setæ 2 mm. long.

Affinity with *E. monocephala*, *concinna*, and *trifoliata*. The sessile leaves tomentose below coupled with the sessile heads with densely tomentose involucres afford good marks of distinction.

Erlangea (§ *Platylepis*) prolixa, sp. nov. *Herba* elata; *caule* robusto ramoso uti rami prominenter costato necnon scabriusculo-pubescente; *foliis* sessilibus oblongo-oblanceolatis obtusis basi leviter amplexicaulibus margine serrato-dentatis chartaceis utrinque scabridis; *capitulis* pro genere majusculis ∞-flosculosis in paniculam laxam oligocephalam scabridam folia longe superantem digestis; *involucri* hemisphærici phyllis 6-serialibus ser. exterioris lanceolatis serr. intermediarum 3 late ovatis rotundatissimis subito apiculato-acuminatis purpureo-marginatis intimis oblongis vel oblongo-linearibus acuminatis; *corollis* breviter exsertis; *achæniis* oblongo-turbinatis 6-costatis microscopice papillosis; *pappi* setis paucis brevibus scabriusculis.

Tanganyika Territory, Kyimbila District; *A. Stolz*, 2616.

Planta saltem 6 dm. alt. Caulis inferne 8 mm. crass. Folia usque 13 × 4 cm., juniora vero multo breviora. Pedunculi proprii plerique 5–8 cm. long., ultimi ± 3 cm. Capitula 1 × 1·5 cm. Involucri phylla extima 4 mm., intermedia 5·5–7 mm., intima 7 mm. long. Corollæ 7 mm. long. tubus compressus inferne angustus papillosusque superne inflatus; lobi oblongi, obtusi, 2 5 mm. long. Achænia uti pappi setæ 1 mm. long.

In general appearance much like *E. monocephala* Muschl., which belongs to § *Bothriocline*. Affinity closest with *E. ugandensis* S. Moore, but with entirely different indumentum, among other features.

Erlangea (§ *Platylepis*) Duemmeri, sp. nov. *Herba* ultrametralis (4 ped. alt.); *caule* erecto superne pauciramoso striato minute tomentello; *foliis* omnibus alternis petiolatis lanceolatis acuminatis apice mucronulatis basi acutis obtusisve margine dentatis basin versus integris membranaceis supra glabris subtus in nervis tomentellis; *capitulis* parvis 13-flosculosis in corymbum sublaxum folia excedentem polycephalum tomentellum dispositis; *involucri* cylindrico-campanulati glabri vel subglabri phyllis 5-serialibus exterioribus ovatis vel ovato-oblongis obtusis interioribus oblongis acutis (intimis acuminatis) anguste scarioso-marginatis; *flosculis* exsertis; *achæniis* plano-convexis facie utraque prominenter tricostatis glabris; *pappi* setis paucis caducissimis.

Uganda, on rocky outcrops at Kiveta; *Dümmer*, 2651 *a*.

Folia pleraque 5–8 × 1·5–2·5 cm., glandulis microscopicis translucentibus præditis; petioli circa 1 cm. long., tomentelli. Inflorescentia circa 12 × 12 cm. Pedunculi proprii 0–3 mm. long. Involucra 5 × 3 mm.; phylla

extima 1–1·5 mm., intermedia 3·5–4 mm., intima usque 5 mm. long. Corollæ lilacinæ, 5 mm. long. Achænia 1·25 mm. long., pappi setæ totidem.

To be inserted next *E. Bagshawei* S. Moore, but the more strongly-toothed leaves have a much less prominent reticulum on the underside, the heads are narrower and with fewer florets, and the inner leaves of the involucre are narrower and acute or acuminate.

ERLANGEA (§ *Eu-Erlangea*) MICROCEPHALA, sp. nov. *Herba* perennis; *caule* lignoso sat valido (3–5 mm. diam.) pubescente ramos multos elongatos floriferos graciles sparsim pubescentes emittente ramis fere a basi corymbiferis corymbis axillaribus bracteatis oligocephalis folia longe excedentibus; *foliis* parvis sessilibus oblongis obtusis utrinque sparsim puberulis; *capitulis* parvulis circa 20-flosculosis; *involucri* campanulati pubescentis phyllis 5-serialibus oblongo-lanceolatis acutis int. quam ext. majoribus; *corollis* breviter exsertis; *achæniis* oblongis plano-convexiusculis circa 8-costatis glabris; *pappi* seta pro flosculo unica sursum barbellata corollæ æquilonga.

Angola, Caculo, Libolo; *Gossweiler*, 6312.

Planta saltem bispithamea. Folia 1·5–2·5 cm. × 3–4 mm. Corymbi plerique 5–10 cm. long.; horum bracteæ 3–14 mm. long. Pedunculi proprii teneri, 1–1·5 cm. long. Capitula 5 × 3·5 mm. Involucri phylla ext. 2–2·5 mm., int. 3·5 mm. long. Corollæ 3 mm. long. Achænia 1·2 mm., pappi seta 3 mm. long.

The small heads and pappus of a single relatively long seta distinguish this plant, which shows an evident approach to *Gutenbergia*.

The pappus of this genus, consisting as it does of setæ detachable on the slightest movement, cannot function as an aid in the diffusion of the fruit. Perhaps it may act as a low palisade round every flower, preventing the corollas being pressed together—in this way it would aid pollination.

## VERNONIA.

VERNONIA (§ *Lepidella*) EYLESII, sp. nov. *Frutex* usque orgyalis, *ramis* sat tenuibus patenti-ascendentibus striatis minute pubescentibus, deinde glabrescentibus; *foliis* parvis subsessilibus ovatis vel ovato-oblongis apice minute mucronulatis basi obtusis integris vel rarissime obscure denticulatis papyraceis supra scabriusculis subtus minute pubescentibus pag. utraque glandulis microscopicis lucentibus inspersis; *capitulis* submediocribus 15-flosculosis in corymbum brevem oligocephalum ramos coronantem digestis; *pedunculis propriis* pubescentibus involucra excedentibus vel subæquantibus; *involucri* subhemispherici 5-serialis phyllis ext. oblongis acutiusculis int. longioribus oblongis obtusis margine anguste scariosis dorso carinatis omnibus dorso puberulis stramineis apice nigris; *corollis* exsertis purpureis; *achæniis* (crudis) subcylindricis basi callosis appresse setulosis; *pappi* squamis abbreviatis linearibus setis scabriusculis albis.

Rhodesia, Makoni District, Forest Hill Kop, 5000–5200 ft.; *Eyles*, 737.

Folia pleraque 15×7 mm., summa vero diminuta (±8×4 mm.). Corymbus circa 3×4 cm. Pedunculi proprii 5–15 mm. long. Capitula pansa circa 1×1 cm. Involucri phylla ext. ±2 mm., int. 3·5–5 mm. long. Corollæ pars angusta 2 mm., pars dilatata 2 mm., lobi 1·5 mm. long. Achænia 2–2·5 mm., pappi squamæ ·4 mm., setæ 4 mm. long.

Close to *V. pandurata* Link, a species with larger amplexicaul leaves, glabrous involucres, and achenes sparsely hairy between the prominent ribs.

VERNONIA (§ *Lepidella*) PROCLIVICOLA, sp. nov. *Herbacea*; *caule* erecto verisimiliter simplici appresse subfulvo-pubescente fere 3 dm. alt.; *foliis* radicalibus oblongo-obovatis apice rotundatis basi in petiolum latum cuneatim angustatis caulinis sparsis (internodiis ±6 cm. long.) subsessilibus oblongo-ovatis vel late oblongis obtusissimis foliis omnibus membranaceis utrinque scabriusculis in costis præsertim pag. inf. scabro-puberulis; *capitulis* submediocribus perpaucis (circa 4) quorum 3 ex axillis foliorum ultimorum abbreviatorum ortis sat longipedunculatis pedunculis pubescentibus; *involucri* 4-serialis late campanulati phyllis anguste lineari-lanceolatis minute nigro-mucronulatis dorso appresse fulvo-sericeis erectis vel paucis exterioribus patulis raro reflexis; *corollis* subinclusis; *achæniis* turbinatis tetragonis angulis sparsim setulosis alibi glanduloso-scabriusculis; *pappi* squamis lanceolatis acutis integris incisisve setis scabriusculis sordide albis.

Belgian Congo, hill-slopes under trees by R. Musofi; *Kassner*, 2686.

Folia radicalia (excluso petiolo 1 cm. long.) usque 6×3·5 cm., exstant equidem minora 3×2 cm. petiolo 5 mm. long.; caulina ±5×3 cm. Pedunculi ±2 cm. long. Capitula pansa 11×15 mm. Involucri phylla extima 5 mm., intermedia 8·5 mm., intima 9 mm. long. Corollæ tubus anguste infundibularis minute glandulosus, 7 mm. long.; lobi lanceolati, 2 mm. long. Achænia 1·5 mm.; pappi squamæ 1 mm., setæ 6 mm. long.

This is one of several species clustering round *V. Petersii* Oliver & Hiern, and *V. ambigua* Kotschy & Peyr. Among these *V. sericolepis* O. Hoffm. is described as having a puberulous stem, differently shaped acute leaves, larger heads with obtuse involucral leaves and longer achenes; *V. clinopodioides* O. Hoffm., with similar achenes to the last, has oblong or narrowly elliptical acute serrate leaves, larger sessile heads, and reflexed involucral leaves, the inner ones almost filiform. *V. fontinalis* S. Moore, with almost identical heads, has different foliage.

VERNONIA (§ *Lepidella*) JELFIÆ, sp. nov. *Herba* erecta circa ⅔-metralis; *caule* subsimplici tetragono subsparsim folioso scabriusculo; *foliis* oblanceolatis obtusis inferne petiolatim attenuatis margine undulato-dentatis pag. utraque scabriusculis superioribus imminutis linearibus; *capitulis* submediocribus circa 40-flosculosis in corymbum laxum oligocephalum paucibracteatum puberulum ordinatis; *pedunculis propriis* tenuibus minute pubescentibus 1–3 cm. long.; *involucri* campanulati phyllis 6-serialibus oblongo-lanceolatis acuminatis dilute viridibus apice purpureis vel fuscis minute pubescentibus; *corollis* breviter exsertis; *achæniis* oblongis 5-costatis costis setulosis; *pappi* squamis laceratis albis setis scabriusculis dilute viridibus.

N.E. Rhodesia, Luivinga, 4500 ft.; *Mrs. Jelf*, 42.

Folia inf. usque 3·5 cm. × 8 mm., superiora circa 2·5 cm. × 3 mm.; folia ramulorum 4 × 1 mm. Inflorescentia circa 10 × 6 cm.; hujus bracteæ anguste lineares, ± 5 mm. long. Involucrum 1 cm. long. et lat.; phylla extima 2–3 mm., intermedia 4–6 mm., intima usque 9 mm. long. Corolla pallide purpurea, anguste infundibularis, puberula, 6·5 mm. long. Achænia basi callosa, adhuc vix matura 1·5 mm. long. Pappi squamæ ·2 mm., setæ 6 mm. long.

Distinguished from *V. chloropappa* Bak., by the smaller heads with narrower less hairy involucral leaves running out into a longish coloured point and the hairy achenes. The involucres also serve as a chief means of distinction from *V. Poskeana* Vatke, var. *chlorolepis* Steetz.

A plant of Gossweiler's (Angola, Cassuango, Kuiriri, No. 3025) seems conspecific. The collector's note states that it is a leafy cæspitose perennial, nearly a metre high and fairly plentifully branched.

VERNONIA (§ *Lepidella*) EXTRANEA, sp. nov. *Herba* circa spithamea; *foliis* amplis ad apicem rhizomatis obesi valde abbreviati rosulatis late obovatis apice rotundatissimis basi in petiolum brevem angustatis margine denticulatis papyraceis utrinque scabriusculis pag. inf. glandulis immersis præditis; *scapo* 1–2-cephalo folia longe excedente fulvo-tomentello; *capitulis* majusculis ∞-flosculosis; *involucri* campanulati phyllis 5-serialibus late ovato-oblongis obtusis nigro-mucronulatis (intimis acuminatis) dorso appresse villosis; *flosculis* breviter exsertis; *achæniis* turbinato-oblongis basi callosis obscure 5-costatis minute sparsim papillosis; *pappi* setis scabriusculis albis squamis anguste acuminatis.

Belgian Congo, slopes of Mt. Kundelungu; *Kassner*, 2707.

Folia 10–11 × 6·5–7·5 cm., in sicco griseo-brunnea. Scapus circa 20 cm. alt. Rhizoma tuberiforme, abunde radicigenum, 2 × 2 cm. Capitula 2 × 2·5 cm. Involucri phylla extima 5–6 mm., intermedia 8–11 mm., intima 13 mm. long. Corollæ pars angusta 6 mm. long., pars dilatata 1·5 × 1 mm. Styli rami 4 mm. long. Achænia 5 mm., pappi squamæ 2 mm., setæ 9 mm. long.

In habit much like *V. gerberiformis* Oliver & Hiern, *V. acrocephala* Klatt, and allied species belonging to § *Decaneuron*. There seems no near affinity for this in § *Lepidella*.

*V. Stuhlmanni* O. Hoffm., ex descript. Tanganyika Territory, Kilosa sub-district; *Swynnerton*, 826.

VERNONIA (§ *Hololepis*) PASCUOSA, sp. nov. *Herba* ultrametralis; *caule* subsimplici erecto fere a basi folioso optime costato scabrido; *foliis* subsessilibus ovatis acutis basi late truncatis vel leviter cordatis margine serrulatis utrinque scabridis; *capitulis* mediocribus ∞-flosculosis singulis terminalibus vel ramulos breves parvifoliosos coronantibus: *involucro* subhemisphærico foliis ultimis reductis arcte stipato phyllis 6-serialibus rigidiusculis lanceolatis (intimis angustioribus) breviter acuminatis margine anguste scariosis puberulis; *corollis* subinclusis; *achæniis* turbinato-cylindricis basi callosis 10-costatis sericeo-setosis; *pappi* setis ext. quam int. scabrida multo brevioribus.

Portuguese Congo, in herb-grown pasturage near Forte Uije; *Gossweiler*, 7404.

Folia circa 5 × 3 cm., juniora ± 3 × 2 cm., summa capitula involucrantia 1–1·5 cm. long., omnia in sicco brunneo-viridia subtus pallidiora; costæ lat. utrinque circa 8, pag. inf. prominentes; petioli 2–3 mm. long., scabridi. Capitula 12 × 15 mm. Involucri phylla ext. ± 5 mm., intermedia circa 10 mm., intima 7 mm. long. Corollæ purpureæ tubus anguste infundibularis papillosus, 7 mm. long.; lobi lineares, 2 mm. long. Achænia 2–2·5 mm., pappi setæ ext. 1 mm., int. 6 mm. long.

Told at once from *V. purpurea* Sch. Bip., by the foliage and the small heads with acuminate involucral leaves.

*V. asterifolia* Bak. Semliki Valley; *Kassner*, 3283. Mubendi Road, 4000 ft.; *Misses E. & C. Godman*, 261.

VERNONIA (§ *Stengelia*) SALTUARII, sp. nov. Verisimiliter *frutex*; *ramis* imprimis sordide tomentosis postea glabrescentibus costasque ostendentibus; *foliis* brevipetiolatis ovato-oblongis acutis basi obtusis margine calloso-dentatis supra scabriusculis subtus dense griseo-tomentosis; *capitulis* submediocribus subsessilibus circa 20-flosculosis in corymbos breves densos oligocephalos digestis; *involucri* campanulati 5-serialis glabri phyllis ext. abbreviatis ovatis crustaceis appendice membranacea obovato-oblonga obtusissima in sicco fusco-brunnea onustis int. sensim longioribus oblongis appendice brevi ovata obtusa donatis; *corollis* breviter exsertis; *achæniis* oblongo-turbinatis 10-costatis puberulis; *pappi* setis scabriusculis dilute stramineis.

Tanganyika Territory, Madolema; *Swynnerton*, 827.

Folia summum 6 × 3 cm. sed sæpe minora, supra in sicco fusca; petioli 3–6 mm. long. Capitula pansa 12 × 12 mm. Involucra 10 × 10 mm.; phylla extima (appendice 1 mm. inclusa) 3 mm. long.; intermedia 3–4 mm. long. (appendice inclusa 8 mm.); interiora 8 mm. (appendice inclusa 9·5–10 mm.) long. Corollæ tubi pars angusta 6 mm. pars ampliata 2 mm., lobi 2 mm. long. Achænia 3 mm., pappi setæ exteriores circa 3 mm., interiores 8 mm. long.

Close to *V. lasiopus* O. Hoffm., but the heads are larger and broader and bear a greater number of florets, while the involucral leaves have broader obtuse appendages.

VERNONIA (§ *Stengelia*) RETIFOLIA, sp. nov. *Herba* bispithamea; *caule* simplice erecto fere a basi folioso subtiliter griseo-tomentoso dein glabrescente; *foliis* sessilibus breviterve petiolatis oblongo-lanceolatis mucronatis basi obtusis vel rotundatis chartaceis supra fere glabris subtus in costa centrali minute griseo-tomentosis pagina utravis præsertim vero inf. arcte reticulatis; *capitulis* paucis majusculis ∞-flosculosis in corymbum foliis breviorem digestis; *involucri* campanulati 4-serialis phyllis inferne chartaceis puberulisque superne appendice ovata dentata dorso pubescente viridi reticulata terminatis; *flosculis* exsertis; *achæniis* (crudis) oblongis basi callosis costatis minute tomentosis; *pappi* setis apice aliquanto complanatis scabriusculis dilute stramineis.

N.E. Rhodesia, Luwingu, 4000 ft.; *Mrs. Jelf.*

Folia pauca inferiora ±3 × 1·5 cm., superiora usque 11 × 3 cm., summa perpauca imminuta in bracteas inflorescentiæ transeuntia; petioli dum adsint summum 5 mm. long. Pedunculi proprii circa 5 mm. long. Capitula 2·8 × 1·8 cm. Involucra 2 × 1·5 cm.; phylla ext. circa 10 mm. long. Appendice 5 × 4 mm., int. 15 mm. Appendice 3 × 3 mm. Corollæ tubi pars angusta 8–14 mm. long., pars ampliata 3·5 mm.; lobi acuti, 2 mm. long. Achænia vix 2 mm., pappus 12 mm. long.

The relatively narrow strongly reticulated leaves, and the involucral leaves with their broad toothed green appendages are the chief marks for the species. Mrs. Jelf notes the florets as being yellow, but this would seem to indicate their later state; when freshly expanded they are most likely white.

VERNONIA (§ *Stengelia*) VENOSA, sp. nov. *Herbacea; caule* folioso erecto valido pluristriato crebro folioso minute griseo-tomentoso; *foliis* approximatis (intermediis 5–15 mm. long.) sessilibus oblongis obtusis basi angustatis calloso-denticulatis pergamaceis supra fere glabris subtus in costis minutissime tomentosis pag. utravis perspicue reticulatis; *capitulis* majusculis brevipedunculatis terminalibus et axillaribus pedunculis bracteis foliis similibus sed multo minoribus summis in phylla involucri transeuntibus involucrumque arcte stipantibus onustis; *involucri* hemisphærici 4-serialis phyllis oblongis crustaceis appendice rotundata venosa minute tomentella onustis interioribus longioribus appendiceque parvula terminatis; *corollis* exsertis; *achæniis* oblongis 10-costatis inter costas breviter setulosis; *pappi* setis minute scabriusculis apice breviter dilatatis dilute stramineis.

Belgian Congo, Kipaila; *Kassner*, 2545.

Folia ±10 × 2·5–3·5 cm., summa circa 5 cm. long., supra in sicco brunneo-viridia nitidaque subtus griseo-viridia. Bracteæ pedunculorum ±2 cm. long., ultimæ involucrum stipantes circa 15 mm. Involucrum 2 × 2 cm.; phylla ext. (appendice 5 × 5 mm. inclusa) circa 10 mm. long., int. usque 18 mm. long. Corollæ tubi pars filiformis 20 mm. long., pars dilatata 5 mm.; lobi triangulares, acuti, 3 mm. long. Achænia 5 mm., pappus 14 mm. long.

The closely arranged strongly reticulate leaves and the heads surrounded by foliaceous bracts (as in § *Hololepis*) are striking features of the species. The affinity is clearly with the plant last described.

VERNONIA (§ *Stengelia*) FULVISETA, sp. nov. *Herbacea, caule* valido sparsim ramoso eximie striato tomentello deinde glabrescente ; *foliis* petiolatis ovatis (paucis junioribus lanceolatis) acutis apice mucronulatis basi truncato-rotundatis calloso-dentatis vel denticulatis membranaceis supra scabriusculis subtus griseo-tomentosis; *capitulis* magnis ∞-flosculosis terminalibus vel ramulos ultimos breves coronantibus ; *involucri* late campanulati 6-serialis phyllis oblongis crustaceis minute tomentellis appendice obovata obtusissima puberula onustis extimis abbreviatis intimis anguste oblongis breviter appendiculatis vel appendice carentibus ; *corollis* exsertis ; *achæniis* subcylindricis basi callosis 10-costatis appresse sericeis; *pappi* setis apice complanatis minuteque serrulatis ceterum glabris rubiginoso-fulvis.

Nyassaland ; *Buchanan*, 1297.

Folia usque 10 × 5·5 cm., sæpius vero minora, *e.g.* ±6 × 2·5 cm., supra in sicco olivaceo-nigra ; petioli 1–5 cm. long., tomentelli. Involucra 2 2 × 3·5 cm.; phylla extima 10 mm. long. (appendice sola 5·5 mm.), intima 12–15 × 2–3 mm.; cetera circa 6 × 3 mm. appendice ±11 × 8 mm. prædita. Corollæ pars filiformis 14 mm., pars ampliata 4 mm. long.; lobi triangulari-oblongi, apice papillosi, 2 mm. long. Achænia 4 mm , pappi setæ 7–11 mm. long.

Allied to *V. Whyteana* Britten, which it resembles in foliage ; but the heads are smaller and the involucral leaves with their appendages much narrower. The achenes, moreover, are more hairy and their ribs not nearly so prominent. The involucral appendages seem to have been green, those of *V. Whyteana* dry very dark brown.

VERNONIA (§ *Lampropappus*) TURBINELLA, sp. nov. *Herbacea*, fere 3-spithamea ; *caule* valido erecto subsimplici subdistanter folioso griseo-tomentoso ; *foliis* brevipetiolatis ovatis vel ovato-oblongis apice basique rotundatis margine repandis supra glabris nitidulisque subtus brunneo- vel griseo-tomentosis utrinque reticulo arcto pag. inf. maxime eminente gaudentibus ; *capitulis* submediocribus corymbum subdensum polycephalum folia circiter æquantem referentibus ; *pedunculis propriis* dense tomentosis bracteis in involucri phylla transeuntibus onustis ; *involucri* turbinati 5-serialis phyllis parvis arcte imbricatis oblongis obtusis dense tomentosis ; *corollis* pappo plane brevioribus inclusis ; *achæniis* turbinatis 5-gonis angulis indumento dense albo-setoso absconditis ; *pappi* setis complanatis rigidiusculis sursum ciliatis stramineis.

Belgian Congo, Musofi River, under trees on hill-slopes; *Kassner*, 2687.

Planta circa 6 dm. alt. Caulis 4–6 mm. crass. Folia summum 10 × 5 cm., sæpius vero 7 × 3·5 cm., summa e ramis brevibus subapicalibus orta imminuta. Inflorescentia 7 × 7 cm. Pedunculi proprii ±15 mm. long., horum bracteæ subulatæ, 2–5 mm. long. Capitula pansa 15 × 10 mm. Involucra 9 × 8 mm.; phylla inter se fere æquilonga, circa 4 mm. long. Corollæ 5 mm. long. Achænia 4·5 mm., pappi setæ 2–8 mm. long.

Recognised on sight from *V. eremanthifolia* O. Hoffm., and *V. lampropappa* O. Hoffm., by the foliage and turbinate heads.

## ELEPHANTOPUS.

Elephantopus Gossweileri, sp. nov. *Herba perennis*; *caulibus* erectis verisimiliter cæspitosis simplicibus hispidulis 1–2-spithameis a basi foliosis fusco-purpureis; *foliis* sessilibus lineari-lanceolatis mucronatis basi in vaginam brevem amplexicaulem dilatatis integris margine revolutis chartaceis pag. utraque scabridis; *capitulis* in glomerulum hemisphæricum foliis summis arcte involucratum compactis; *foliis involucrantibus* exterioribus ceteris similibus sed paullo brevioribus interioribus gradatim imminutis intimis linearibus sursum setosis fere omnibus basi insigniter dilatatis; *receptaculo communi* concaviusculo setifero; *capitulis* propriis oblongis 3–4-flosculosis; *involucri* phyllis circa 7 lineari-lanceolatis acutis glabris ext. quam int. paullo brevioribus int. corollis subæquilongis; *corollæ* tubo angusto limbo 5-lobo; *achæniis* lineari-oblongis basi contractis callosisque setaceo-sericeis obscure costatis; *pappi* setis pluribus ext. paucis quam ceteræ parum brevioribus scabriusculis stramineis.

Angola, Cuanza Norte District, Samba Caju, 900 m.; *Gossweiler*, 8478.

Folia pauca inf. 6 cm. × 7 mm., cetera 8–10 cm. × 6 mm., in sicco griseo-viridia, subtus glandulis immersis inspersa. Folia involucrantia ext. circa 6 cm. long, horum basis dilatata fusca ciliata 1 cm. × 8 mm. Glomeruli 2–2·5 × 3–3·5 cm. Capitula 10 × 3 mm.; phylla ext. 9 mm., int. 7·5 mm. long. Corollæ tubus 6·5 mm., lobi 2 mm. long. Achænia 3-4 mm., pappus 6 mm. long.

The sparser hairiness, smaller leaves, and relatively short involucrating leaves are readily noticed peculiarities of this species as compared with *E. senegalensis* Oliver & Hiern, and *E. multisetosus* O. Hoffm. In addition, the achenes of the former are broader and shorter, while those of the latter, according to the description, are longer and the pappus is nearly double as long. The corolla of *E. senegalensis* was not seen by Oliver and Hiern; that of the other is twice as long as ours.

Elephantopus vernonioides, sp. nov. *Herba* circa spithamea; *caule* erecto simplici fere a basi folioso costato piloso-hispidulo; *foliis* sessilibus lanceolatis obtusiusculis basi dilatatis amplexicaulibusque integris firme membranaceis pag. sup. scabridis pag. inf. præsertim in nervis pilis hispidis appressis obsitis; *glomerulo* capitulorum hemisphærico foliis summis arcte involucrato; *foliis involucrantibus* basi leviter dilatatis ext. foliis caulinis similibus sed parum brevioribus int. imminutis lineari-lanceolatis acutis piloso-hispidis; *receptaculo communi* plano setoso; *capitulis* anguste ovoideo-oblongis 4-flosculosis; *involucri* phyllis circa 7 ext. abbreviatis late triangularibus acutis int. multo longioribus cymbiformibus apiculatis glabris; *corollæ* tubo tenui sursum leviter ampliato limbo 5-lobo; *achæniis* oblongis setosis; *pappi* setis pluribus scabriusculis stramineis.

Angola, Cuanza Norte District, in herb-grown *Andropogon* beds at Capijongo; *Gossweiler*, 7461.

Internodia ± 1 cm. long. Folia usque 8 × 1·5 cm., sed plerumque minora, *e.g.* 6 × 1·2 cm. Folia involucrantia ext. 2·5–4 cm., int. ± 1·5 cm. long. Capitula 9 × 4 mm.; phylla ext. circa 3 mm., int. 8 mm. long. Corollæ tubus 10 mm., lobi 3·5 mm. long. Achænia 2 mm., pappus 8 mm. long.

A very distinct species: the foliage and short involucrating leaves are specially worthy of notice.

## HELICHRYSUM.

HELICHRYSUM (*Argyreia* § *Paniculata*) PALLENS, sp. nov. *Herba* perennis circa bispithamea; *caule* erecto a basi folioso griseo-araneoso; *foliis* sessilibus breviter amplexicaulibus oblongo-lanceolatis obtuse acutis obscure trinervibus pag. utravis tela araneoso-tomentosa grisea arcte indutis; *capitulis* submediocribus homogamis circa 40-flosculosis in corymbum foliis plane vel breviter longiorem bracteis paucis foliis similibus nisi minoribus onustum araneoso-tomentosum ordinatis; *involucri* campanulati 5-serialis glabri phyllis lanceolatis acutis sordide albis nitidis; *receptaculo* plano alveolato; *corollis* 5-lobis; *achæniis* oblongis microscopice papillosis; *pappi* setis circa 25 corollis longioribus scabriusculis albis.

Angola, Munongue, in short thicket-grown pasturage; *Gossweiler*, 2485.

Folia 4·5–7 × 1–1·4 cm., summa in bracteas inflorescentiæ transeuntia 3–3·5 cm. long. Inflorescentia usque 8 × 7 cm. Involucra 8 × 10 mm.; phylla extima 3 mm., intermedia 5–6 mm., intima 7 mm. long. Corollæ (limbo incluso) 3·5–4 mm., pappus 6 mm., achænia ·6 mm. long.

Apparently this should come next to *H. sordescens* DC., which it fairly well resembles in flower-heads, but the foliage is quite distinct, as is the habit.

*H. nitens* Oliver & Hiern. In open grassy Cæsalpineous woods between Mt. Amaral and Forte Maria Pia; *Gossweiler*, 1823. Cuanza District, in wet situations amongst reeds and grasses on the road between Camabatela and Quitomba; *Id.*, 7399. Both of these differ from the ordinary form in having the leaves scattered up the stem, instead of most of them being collected at its base, a difference Moeser makes of some importance in his clavis (Bot. Jahrb. xliv. p. 325). But except for this there seems no difference worthy of notice.

HELICHRYSUM (*Chrysolepidea* § *Xerochlæna*) RUGATUM, sp. nov. *Herbacea*; *caule* e rhizomate lanoso 1 cm. diam. erecto omnimodo folioso tomentoso; *foliis* sessilibus oblongis (perpaucis inferioribus oblongo-obovatis) obtusis basi laxe amplexicaulibus subevanide trinervibus supra mox araneoso-pubescentibus subtus tomentosis; *capitulis* majusculis heterogamis ∞-flosculosis paucis (in exempl. unico viso 4) ad apicem caulis pedunculis brevibus tomentosis insidentibus; *involucri* campanulati phyllis pluriseriatis ovato-oblongis (interioribus oblongo-linearibus intimis linearibus) acutis integris vel sursum erosis exterioribus transversim rugatis omnibus aureo-brunneis nitidisque; *receptaculo* alveolato; *flosculis* inclusis paucis extimis ♀; *corollis* 5-lobis;

*achæniis* oblongis glabris; *pappi* setis pluribus basi liberis scabriusculis sordide albis.

Belgian Congo, Mt. Kundelungu, under trees; *Kassner*, 2729.

Planta sesquispithamea. Folia inf. ±8×2 cm., superiora sensim minora, summa modo 3–3·5 cm. long. Pedunculi 1·5–2 cm. long. Capitula 1·8×2 cm. Involucri phyllo ext. 7–10 mm., intermedia 14 mm., intima 15 mm. long. Corollæ 3 mm., achænia (cruda) 1 mm., pappus 3·5 mm. long.

Affinity with *H. squamosum* Thunb.; still more like *H. xerochrysum* DC., which, however, belongs to *Lepicline*. The heads resemble those of some spp. of the Australian genus *Podolepis*, notably *P. rugata* Labill.

HELICHRYSUM (*Chrysolepidea* § *Xerochlæna*) KUNDELUNGENSE, sp. nov. *Herba* circa sesquispithamea, caulibus simplicibus tenuibus a basi foliosis laxe araneosis; *foliis* crebris (internodiis circa 5 mm. long.) sessilibus oblongo-lanceolatis apiculatis basi breviter amplexicaulibus trinervibus utrinque sed præsertim pag. inf. tomentosis; *capitulis* submajusculis heterogamis ∞-flosculosis paucis ad apicem caulis approximatis (nonnunquam solitariis) pedunculis bracteatis tomentosis capitulis circa æquilongis; *involucri* campanulati phyllis pluriseriatis oblongo-lanceolatis (intimis linearibus) breviter acuminatis læte aureis nitidis; *receptaculo* alveolato; *flosculis* inclusis paucis extimis ♀; *corollis* 5-lobis; *achæniis* oblongis glabris; *pappi* setis pluribus scabriusculis sordide albis.

Belgian Congo, Kundelungu, on banks of streams; *Kassner*, 2747.

Folia pleraque 2·5 cm.×7–10 mm., summa leviter imminuta. Pedunculi 1–1·5 cm. long. Capitula 12×14 mm. Involucri phylla extima 4–5 mm., intermedia 7–9 mm., intima 10 mm. long. Corollæ 3·5 mm., achænia (cruda) 1 mm., pappus 4 mm. long.

Allied to the S. African *H. decorum* DC., but a weaker-growing plant, with smaller leaves and heads, the latter with shortly acuminate involucral leaves.

HELICHRYSUM (*Chrysolepidea* § *Xerochlæna*) KASSNERI, sp. nov. *Herba* perennis; *caulibus* spithameis simplicibus ascendentibus a basi usque ad inflorescentiam crebro foliosis albo-tomentosis; *foliis* sessilibus lineari-oblanceolatis apiculatis basi breviter amplexicaulibus uninervibus supra araneosis subtus tomentosis; *capitulis* submediocribus heterogamis ∞-flosculosis corymbum terminalem brevem oligocephalum efficientibus; *involucri* campanulati phyllis pluriseriatibus lanceolatis acutis (intimis linearibus) nitidis aureis extimis breviter aeneo-tinctis; *receptaculo* convexiusculo minute alveolato; *flosculis* paucis extimis ♀; *corollis* 5-lobis inclusis; *achæniis* oblongis glabris; *pappi* setis sursum scabridis sordide albis.

Belgian Congo, Mt. Senga; *Kassner*, 2962.

Internodia ±5 mm. long. Folia pleraque 2–2·5 cm.×4–5 mm., infima magis approximata modo 7 mm. long. Corymbus 1·5–2×3–3·5 cm. Pedunculi 5–15 mm. long.; horum bracteæ paucæ, foliis similes sed multo minores. Capitula 7 × 7 mm. Involucri phylla ext. 3–3·5 mm., int. 4·5–6·5 mm., intima pauca modo 2·5 mm. long. Corollæ dimidio inf. inflatæ, 2 mm. long. Achænia (cruda) ·4 mm., pappus 2·5 mm. long.

Near the last, but with narrower one-nerved leaves and considerably smaller heads. De Wildeman and Muschler (Ann. Mus. Congo Belge, sér. 4, i. p. 166) refer this to *H. Buchanani* Engl., which differs from it in several respects.

HELICHRYSUM (*Chrysolepidea* § *Stœchadina*) UMBELLULATUM, sp. nov. *Herba* perennis erecta circa trispithamea; *caule* simplici fere a basi folioso griseo-araneoso-tomentoso; *foliis* sessilibus oblongo-oblanceolatis breviter amplexicaulibus trinervibus supra araneosis postea glabris nitidulisque subtus griseo-tomentosis; *capitulis* parvis sessilibus homogamis 10-flosculosis in umbellas longipedunculatas ± 8-cephalas corymbum laxum folia facile superantem referentes digestis; *involucri* cylindrici ima basi leviter araneosi phyllis 5-serialibus oblongis acutis basi crustaceis arcte imbricatis nitidis dilute albo-brunneis intimis apice albis; *receptaculo* plano nudo; *corollis* 5-lobis; *achæniis* cylindricis papillosis; *pappi* setis circa 20 scabridis albis.

Benguela, in woods at Anha; *Gossweiler*, 3639.

Folia pleraque 6–10 × 1·5–3 cm., tenuiter coriacea. Inflorescentia 20 × 13 cm.; pedunculi umbellorum plerumque 1–3 cm. long., leviter araneosi. Capitula 7 × 3–4 mm. Involucri phylla ext. 2·5–3 mm., int. 4 mm. long. Corolla 2·5 mm., pappus 3·5 mm. long. Achænia ·5 mm. long.

No. 4430, in Mumua woods between Kakonda and Bissagra, is conspecific.

Affinity with *H. stramineum* Hiern, and *H. congolanum* Schlechter & O. Hoffm.

HELICHRYSUM (*Chrysolepidea* § *Stœchadina*) CONCURSUM, sp. nov. *Herba* perennis cæspitosa; *caule* erecto subsimplici a basi usque ad medium bene foliato argyreo-tomentoso; *foliis* sessilibus oblongo-lanceolatis obtuse mucronulatis deorsum amplexicaulibus 3–5-nervibus superioribus multo minoribus plerisque ramis applicatis apice ipso sæpe breviter recurvis omnibus pag. sup. glabris nitidulisque pag. inf. argyreo-tomentosis; *capitulis* parvis homogamis 8-flosculosis dense globoso-cymosis cymis solitariis terminalibus bracteatis; *bracteis* scariosis lanceolatis acuminatis; *involucri* cylindrico-turbinati phyllis circa 5-serialibus arcte imbricatis haud radiantibus oblongis acutis intimis minoribus obtusis scariosis superne aureis; *receptaculo* plano nudo; *corollis* 5-lobis; *achæniis* (crudis) subquadratis glabris; *pappi* setis 8 corollam breviter superantibus basi filiformibus inde complanatis apice breviter barbellatis.

Angola, between the rivers Kului and Kubango in herb-grown secondary mixed woods; *Gossweiler*, 2152.

Planta bispithamea. Folia circa 6 cm. × 8–9 mm., supra in sicco griseo-brunnea, superiora ± 2 cm. × 3–4 mm.; ultima in bracteas inflorescentiæ transeuntia. Cymæ 13 mm. diam.; harum bracteæ summum 6 mm. long.

Capitula 4·5 × 2 mm. Involucri phylla ± 4 mm. long., intima modo 2·5 mm. Corolla 1·5 mm., achænia ·5 mm., pappi setæ 1·75 mm. long.

Nearest *H. subglomeratum* Less., but the habit and foliage are those of *H. coriaceum* Sond.

HELICHRYSUM (*Lepicline* § *Plantaginea*) OLIGOCEPHALUM, sp. nov. *Herba* perennis, ascendens, fere 2-spithamea, rhizomate abunde radicigero; *caule* sat tenui paucifoliato superne nudo tela araneosa arcta obsito; *foliis* radicalibus lanceolatis obtusis petiolo alato insidentibus caulinis perpaucis lanceolatis obtusis late amplexicaulibus omnibus trinervibus supra fuscis scabriusculisque subtus griseo-tomentosis; *capitulis* homogamis submediocribus circa 50-flosculosis in corymbum laxum oligocephalum digestis; *involucri* late campanulati sparsim araneosi 5-serialis phyllis oblongis obtusis (intimis linearibus) scariosis brunneis sursum sordide brunneo-albis; *receptaculo* subplano fimbrillis lineari-lanceolatis achænia superantibus onusto; *achæniis* subquadratis papillis perspicuis albis obsitis; *pappi* setis circa 20 ima basi connatis corollis æquilongis scabriusculis albis.

Angola; *Gossweiler*, 2249.

Folia radicalia (petiolo incluso) usque 6 cm. long., caulinorum 2 visorum majus 7·5 × 1·5 cm., minus 2·5 cm. long. Inflorescentia 10 × 5 cm.; pedunculi proprii graciles, 1–3 cm. long. Capitula 7 × 9 mm. Involucri phylla extima 3 mm., intermedia usque 4·5 mm., intima 5 mm. long. Receptaculi paleæ 1·75 mm. long. Corollæ 4 mm., achænia 1 mm., pappus 4 mm. long.

Known from its allies *H. latifolium*, *undatum*, etc., by the open few-headed inflorescences, and the campanulate many-floretted heads with brown involucres.

HELICHRYSUM (*Lepicline* § *Plantaginea*) PASCUOSUM, sp. nov. *Herba* perennis trispithamea; *caulibus* cæspitosis a basi fere ad inflorescentiam foliosis erectis sæpe leviter anfractuosis araneoso-tomentosis; *foliis* lineari-lanceolatis apice uncinulato-mucronatis basi amplexicaulibus breviterque decurrentibus trinervibus tenuiter coriaceis supraglabris in sicco fuscis subtus argyreo-tomentosis; *capitulis* parvis 25-flosculosis in corymbum laxissimum suboligocephalum paucibracteatum tomentosum dispositis; *involucri* campanulati fere glabri (levissime araneosi) 3-serialis phyllis obovato-oblongis (intimis oblongis) obtusis inferne crustaceis superne dilute brunneis; *receptaculo* plano fimbrillis oblongis acutis achæniis æquilongis; *achæniis* cylindricis glabris; *pappi* setis circa 20 scabriusculis albis.

Angola, Kului, in short thicket-grown pasturage near Forte Dom Affonso; *Gossweiler*, 2902.

Folia pleraque 3·5–4·5 cm. × 3–6 mm., perpauca summa ± 3 cm. long. Inflorescentia usque 10 × 26 mm.; bracteæ lineares, ± 1 cm. long. Capitula 6 × 6 mm. Involucri ser. i. 2·5 mm., ser. ii., iii. 4 mm. long. Corollæ 3·5 mm. Achænia 1·25 mm., pappus 3·25 mm. long.

In habit and foliage remarkably like *H. coriaceum* Sond. The effuse inflorescence and smaller almost glabrous heads with obtuse involucral leaves are the salient features.

No. 2245 from near Katoco River belongs here. The inflorescence is narrower (some 9 × 10 cm.). Its flower-heads are not quite mature.

One would have wished to make use of Moeser's classification in his laborious memoir (Engl. Bot. Jahrb. xliv. (1910) pp. 239–345); but his arrangement, comprising no less than 43 divisions, was found to be too complicated in practice.

## INULA.

INULA (*Bojeria*) OLIGOCEPHALA, sp. nov. *Herba* bispithamea in sicco griseo-fusca; *caule* erecto juxta apicem pauciramoso optime sulcato sparsim hirsuto; *foliis* infimis e basi caulis ortis petiolatis oblongo-obovatis obtusis basi angustatis dentatis utrinque pilis hispidis fulvis appressis subsparsim obsitis foliis reliquis sessilibus oblongis obtusis basi rotundatis plerisque breviter amplexicaulibus; *capitulis* majusculis homogamis ad apicem ramorum brevium (in exempl. scrutato 3) solitariis; *involucri* late campanulati 5-serialis phyllis oblongis lanceolatis obtusis inferne coriaceis superne firme membranaceis dorso margineque pilio hispidulis onustis intimis anguste linearibus acuminatis apice ciliatis; *corollis* inclusis anguste infundibularibus 5-lobis; *antherarum* caudis sparsim ramulosis; *styli* ramis clavellatis; *achæniis* (crudis) linearibus pluricostatis glabris; *pappi* setis paucis glabris dilute stramineis.

Angola, in short thicket-grown pasturage near Kakonda; *Gossweiler*, 4328.

Folia radicalia 20 × 8 cm.; petioli sparsim hirsuti, 2·5–4 cm. long.; caulina ± 6 × 3 cm., penultima usque 2 cm. diminuta, ultima in involucri phylla transeuntia. Involucra 2 × 3 cm.; phylla 12–14 mm. long., ext. 3 mm. lat. Corolla 7 mm. long., lobi 2 mm. Achænia 2 mm., pappi setæ 4–5 mm. long.

INULA (*Bojeria*) GIMBUNDENSIS, sp. nov. *Herba* scapigera; *foliis* ad apicem caulis brevissimi obesi appresse villosi rosulatis ovatis vel ovato-oblongis apice rotundatissimis basi in petiolum villosum angustatis dentatis pergamaceis supra scabriusculis pilis strigosis appressis basi dilatatis inspersis subtus in nervibus hirsutulis; *capitulis* submediocribus homogamis in corymbum apertum oligocephalum scapum folia facile excedentem paucibracteatum inferne fulvo-hirsutum superne scabridum terminantem digestis; *involucri* companulati 5-serialis phyllis oblongis obtusis (intimis linearibus acuminatis) ciliatis coriaceis; *flosculis* inclusis; *corollis* anguste tubulosis breviter 5-lobis; *antherarum* caudis subsimplicibus; *styli* ramis clavellatis; *achæniis* (crudis) linearibus pluricostatis sursum sparsim setulosis; *pappi* setis paucis scabriusculis dilute stramineis.

Angola, in humid woods at Gimbundo ; *Gossweiler*, 3814.

Folia usque 20–22 × 11–12 cm., alia modo circa 10 × 6–7 cm., in sicco læte viridia ; costæ (uti reticulum) pag. inf. optime visæ ; petioli 1–2·5 cm. long. Scapus 5–6 dm. attingens ; hujus bracteæ inf. oblongo-oblanceolatæ, 4–10 cm. long., sup. gradatim abbreviatæ, ultimæ in involucri phylla transeuntes. Corymbus circa 9–10 × 10–16 cm. Capitula 11 × 12 mm. Involucri phylla ext. 4–5 mm., int. 6 mm., intima 7·5 mm. long. Corolla 4·5 mm., achænia 2 mm , pappi setæ 3–4 mm. long.

This is close to *I. huillensis* Hiern. The broad foliage leaves and much smaller capitula with oblong leaves are the chief features.

## SPHACOPHYLLUM.

SPHACOPHYLLUM GOSSWEILERI, sp. nov. *Herba* perennis, ramosa ; *ramis* subteretibus striatis minute scabriusculo-pubescentibus ; *foliis* petiolatis ambitu oblongis obtusis pinnatifidis segmentis obtusis utrobique scabriusculis ; *capitulis* submediocribus in corymbum oligocephalum foliis multo longiorem digestis ; *pedunculis propriis* elongatis tenuibus scabriusculis ; *involucri* phyllis 3-serialibus oblongis obtusiusculis sursum herbaceis scabriusculis ; *receptaculi* paleis integris anguste linearibus acutiusculis ; *ligulis* circa 20 oblongis ex involucro eminentibus ; *corollis disci* inferne angustatis ; *antherarum* caudis brevibus ; *achæniis* compressis oblongis (basi paullulum angustatis) 4-costatis glabris ; *pappo* obsoleto.

Angola, on ant-hills near Kakonda, *Gossweiler*, 3337.

Foliorum lamina 1–3 cm. × 7–15 mm. (petiolis 5–12 mm. long. exclusis). Pedunculi proprii inf. 5–8 cm. long., sup. breviores. Capitula 6 × 8 mm. Involucri phylla 3 mm. long. Receptaculi paleæ 3 mm., ligulæ 3 mm., corollæ disci 3 mm. long., achænia vix 1 mm.

Distinguished from *S. pinnatifidum* O. Hoffm., chiefly by the narrow involucral leaves, the differently shaped ligules, and the longer corollas greatly narrowed below. It is still nearer *S. Lastii* O. Hoffm., which, with much the same foliage, has hairy involucres, broad concave receptacular paleæ, and larger and broader ligules.

No. 2691 from Massaca, Rio Kuelai, is probably conspecific, but the material is unsatisfactory.

SPHACOPHYLLUM PRATENSE, sp. nov. *Herba* cæspitosa, spithamea ; *caulibus* ascendentibus foliosis scabriusculo-puberulis ; *foliis* radicalibus longe gracileque petiolatis ovato-oblongis obtusis basi in petiolum angustatis margine crenatis foliis caulinis radicalibus similibus nisi minoribus breviusque petiolatis omnibus utrinque scabriusculis in sicco fuscescentibus ; *capitulis* submediocribus terminalibus vel ex axillis ortis solitariis longipedunculatis ; *involucri* 3-serialis phyllis late oblongis acutiusculis dorso scabriusculis ; *receptaculi* paleis concavis lineari-lanceolatis acutis integris vel trilobis sursum ciliolatis; *ligulis* fere 20 exsertis obovato-oblongis; *corollis* disci infundibularibus; *antherarum* caudis brevibus; *achæniis* oblongis 5-costatis epapposis glabris.

Angola, in wet meadows at Dongo near Kuelai; *Gossweiler*, 3335.

Folia radicalia usque 4 × 1·5 cm., petiolo circa 4·5 cm. long., sæpius vero minora; caulina ±2 × 1·5 cm., summa reducta. Pedunculi plerique 7–10 cm. long. Capitula 6 × 10 mm. Involucri phylla 4 mm. long.; ligulæ vix 3 mm.; receptaculi paleæ 3 mm., achænia (cruda) 1 mm. long.

Near *S. Ruchwaldi* O. Hoffm., the cæspitose habit, long-stalked crenate radical leaves, smaller heads, and shorter ligules are characteristic features.

SPHACOPHYLLUM SPILANTHOIDES, sp. nov. *Herbacea*, gracilis; *foliis* (perpaucis solum visis) ambitu ovatis vel oblongis obtusis basi attenuatis pinnatisectis ultimis nonnunquam subintegris scabriusculis in sicco viridibus; *capitulis* parvis longipedunculatis solitariis terminalibus vel ex axilla fol. supremi oriundis pedunculis tenuibus uti ramuli striati scabriusculis; *involucri* phyllis 2-serialibus ext. ovato-oblongis obtusis quam int. obovato-oblonga obtusissima brevioribus omnibus sursum herbaceis scabridisque; *receptaculi* conoidei paleis cymbiformibus acutis flosculos amplectentibus; *ligulis* pluribus longe exsertis ovato-oblongis retusis; *corollis disci* infundibularibus; *antherarum* caudis minutis; *achæniis* oblongis compressis 5-costatis brevissime setulosis; *pappi* squamis minutis cupulatis apice liberis addita plerumque arista quam cupula paullulum breviore.

N.E. Rhodesia, S. of Lake Tanganyika; *Rev. E. H. Clark.*

Folia usque 2 cm. long.; horum lobi dum adsint oblongi, 4–8 mm. long. Pedunculi 4·5–7 cm. long. Capitula 8 mm. diam. Involucri phylla ext. 2·5 mm., int. 3·5 mm. long. Receptaculi paleæ 3 mm.; ligulæ vix 5 mm.; disci corollæ 2 mm.; achænia 1·5 mm. long.

According to O. Hoffmann's too short description unaccompanied by measurements, this must be near his *S. Stuhlmanni*, the pappus of the two being, measurements apart, very similar; but, inasmuch as he describes the leaves as ovate and crenate-dentate, while the receptacular paleæ are acuminate, *S. Stuhlmanni* would seem to be different from the present plant. Mr. Clark's specimens unfortunately are only fragments. The heads, it may be remarked, look much like those of some species of *Spilanthes*. The conical receptacle is worthy of notice.

SPHACOPHYLLUM TENERUM, sp. nov. *Herba* 1–2-spithamea; *caule* subsimplici debili distanter folioso leviter scabriusculo; *foliis* parvulis petiolatis ovatis obtusis basi obtusissimis margine crenulatis vel fere integris scabriusculis; *capitulis* parvulis homogamis terminalibus; pedunculis elongatis fere ebracteatis; *involucri* 3-serialis phyllis ext. lanceolatis reliquis ovato-oblongis obtusis vel truncatis dentatis ciliolatis; *receptaculi* paleis cymbiformibus obtusis flosculos arcte amplectentibus; *corollis* anguste campanulatis; *antherarum* caudis valde abbreviatis; *achæniis* subteretibus oblongis obscure costatis glabris; *pappo* 0.

Nyassaland; *Buchanan,* 651 (of 1891 coll.).

Folia 5–15 × 4–7 mm., petioli gracillimi, plerique 3–7 mm. long. Involucri phylla ext. 1·5 mm., cet. 2–2·5 mm. long. Capitula 5–6 mm. diam. Receptaculi paleæ 2 mm., corollæ ægre 2 mm., achænia nigra vix 1 mm. long.

Nearest *S. Holstii* O. Hoffm., but different in habit, small leaves, involucre, and receptacular paleæ.

## ANISOPAPPUS.

Anisopappus Davyi, sp. nov. *Herba* ascendens, ramosa; *ramis* sparsim et distanter foliosis striatis scabriusculis; *foliis* parvulis sessilibus anguste lineari-spathulatis basi longe attenuatis ita petiolum referentibus integris utrobique scabriusculis; *capitulis* mediocribus longipedunculatis ramos vel ramulos solitatim terminantibus pedunculis bracteis paucis filiformibus onustis; *involucri* late campanulati phyllis 3-serialibus lanceolatis (extimis linearibus) acutis (intimis breviter acuminatis) sursum herbaceis scabriusculis; *receptaculi* paleis lineari-lanceolatis acutis concavis corollis circa æquialtis; *ligulis* fere 20 breviter exsertis late oblongis; *antherarum* caudis minutis; *achæniis* subcylindricis 5-costatis breviter setulosis; *pappi* corona brevissima additis setis circa 6 multo longioribus inter se inæquilongis.

Katanga, Kambwe Mine, near Elisabethville; *Burtt Davy*, 18041.

Planta circa sesquispithamea. Folia ±15 mm. long., 1·5–2·5 mm. lat., in sicco fusco-grisea. Pedunculi 10–15 cm. long. (raro modo 5 cm.); horum bracteæ circa 5 mm. long. Capitula 6 × 12 mm. Involucri phylla ext. 4 mm., int. 5 mm. long. vel paullo longiora. Receptaculi paleæ ciliolatæ, 4 mm. long. Ligulæ 4 mm., achænia 1·5 mm., pappi setæ ·75–1·25 mm. long.

A very distinct species known on sight by the small narrowly spathulate leaves.

## GEIGERIA.

Geigeria affinis, sp. nov. *Herba* perennis, ramosa; *caulibus* e rhizomate pennæ corvinæ crassitudine cæspitosis aperte ramosis ramis debilibus procumbentibus dichotomis aliquanto ancipitibus mediocriter foliosis glabris; *foliis* elongatis planis anguste linearibus obtusis decurrentibus integris vel hinc inde minute denticulatis glabris; *capitulis* submediocribus pluriflosculosis solitariis inferioribus in furcis ramorum sessilibus ceteris lateralibus; *involucri* anguste campanulati phyllis 5-serialibus ext. ovato-lanceolatis dorso carinatis apice in appendicem linearem herbaceam exeuntibus int. lanceolato-oblongis acutis apice breviter barbellatis omnibus tenuiter coriaceis; *ligulis* circa 15 bene exsertis; *achæniis* turbinatis villosis; *pappi* squamis 10 obovatis ext. obovatis int. in aristam quam se ipsæ longiorem desinentibus.

Angola, in fissures among ferruginous rocks between the Forte Princeza Amelia and Rio Kubango; *Gossweiler*, 3555.

Planta sesqui-bispithamea. Rami 1–2 mm. lat. Folia 4–7 cm. long., 1–2 mm. lat., in sicco fusca. Capitula pansa 12 mm. diam. Involucri phylla ext. 5–6 mm. long. exclusa appendice plerumque 3–5 mm.; phylla int. 8·5 mm. long., pauca intima 7·5 mm. long., hæc margine inciso-ciliata. Ligulæ oblongæ, 8 mm. long., disci corollæ totidem. Achænia 1 mm., pappi squamæ ext. ·5 mm., int. (cum arista) 2 mm. long.

Affinity with *G. Zeyheri* Harv. The absence of hairs, the flat (not involute) leaves, and the narrower heads are the chief features.

GEIGERIA ASPALATHOIDES, sp. nov. *Suffrutex* ultraspithameus; *caulibus* procumbentibus cæspitosis e rhizomate lignoso robusto ortis omnimodo crebro foliosis; *foliis* approximatis sessilibus breviter decurrentibus lineari-subulatis spinuloso-acuminatis tenuiter coriaceis minute puberulis costa media costisque 2 submarginalibus optime perspicuis percursis; *capitulis* mediocribus terminalibus solitariis discoideis foliis ultimis arcte stipatis; *involucri* campanulati phyllis 4-serialibus lineari-lanceolatis acuminatis herbaceis margine ciliolatis; *corollis* circa 30 exsertis; *achæniis* turbinatis villosis; *pappi* paleis 20 lanceolatis vel oblanceolato-oblongis acutis vel obtusis varie incisis exterioribus quam interiora interdum aristata paullo brevioribus.

Angola, Kubango, in open thickets on red gravelly soil near Forte Princeza Amelia; *Gossweiler*, 4177.

Rhizoma usque 2 cm. diam. Folia pleraque 1–1·5 cm. long., basi 2 mm. lat. vel paullulum ultra. Capitula 15 mm. diam. Involucri phylla 10 mm. long. Corollæ 9 mm. long. Achænia 2 mm., pappus 1 mm. long.

This is undoubtedly near *G. foliosa* O. Hoffm. & Muschl., but, according to the description, differs in involucre and pappus. The scales of the pappus being much incised and sometimes almost to the bottom, it is no easy task to ascertain their number, but the description given above is believed to be correct.

No. 3553 from the same locality, with somewhat shorter and broader leaves, is conspecific.

GEIGERIA PTEROPODA, sp. nov. *Fruticulus* ramosus ultrametralis; *ramis* rigidis gracilibus sat bene foliosis anguste sed perspicue alatis deinde subteretibus glabris; *foliis* sessilibus linearibus obtusis tenuiter coriaceis pag. inf. furfura minuta fulva indutis; *capitulis* pro genere submediocribus ramulos solitatim terminantibus foliis ultimis diminutis stipatis; *involucri* turbinato-cylindrici phyllis 6-serialibus oblongis obtusis apice induratis coriaceis nitidulis; *ligulis* paucis bene exsertis; *corollis disci* circa 30; *achæniis* turbinatis albo-villosis; *pappi* paleis 10 lanceolatis ext. acutis integris vel subintegris quam int. breviter fimbriata in setam sat longam excurrentia brevioribus.

Angola, Kubango, in fissures of rocks in a conglomerate of brown ironstone near Forte Princeza Amelia; *Gossweiler*, 1969.

Ramulorum alæ circa 2 mm. lat., reticulato-venosæ. Folia pleraque 2–3 cm. × 2–3 mm., utrinque glandulis microscopicis lucentibus subsparsim prædita. Capitula pansa 10 × 6 mm. Involucri phylla extima 4–4·5 mm., intermedia 6–6·5 mm., intima 7 mm. long. Ligulæ oblongo-ovatæ, 5 mm. long. Corollæ disci ægre 7 mm. long. Achænia 1 mm., pappi squamæ ext. 1·5 mm., int. 2 mm. long.

The narrowly winged branches, narrow leaves, and smaller turbinate heads serve to distinguish this on sight from *G. angolensis* O. Hoffm.

Geigeria obovata, sp. nov. *Herba* vix spithamea, rhizomate lignoso usque 7 mm. diam.; *caule* subsimplici (hac atque illac ramulos perbreves parvifoliosos emittente) fere a basi folioso puberulo alato alis integris; *foliis* crebris (internodiis ± 7 mm. long.) parvis sessilibus oblongo-obovatis acute mucronatis obscure denticulatis firme membranaceis utrinque puberulis; *capitulis* submediocribus circa 14-flosculosis ad apicem caulis 2–3-nis; *involucri* anguste campanulati puberuli phyllis 5-serialibus ext. late oblongis in appendicem oblongam sursum reflexam apice mucronatam exeuntibus coriaceis int. oblongo-lanceolatis acutis erectis ciliatis tenuiter coriaceis quam ext. longioribus; *achæniis* turbinatis appresse setulosis; *pappi* squamis 10 ovatis ext. muticis int. breviter aristatis.

Angola, Kubango, between Forte Colui and Sinbula Lanolingo; *Gossweiler*, 2150.

Caulis alæ 2 mm. lat., reticulato-venosæ. Folia ± 2·5 × 1 cm., utrinque reticulato-venosa. Capitula 12 × 7 mm. Involucri phylla ext. 4·5–6 mm. long., int. 8 mm. Corollæ 7·5 mm. long. Achænia 1 mm. long, pappus totidem.

Distinguished from *G. Wellmanii* Hutchins., chiefly by the short and broad leaves and the pappus with awned inner scales.

## ASPILIA.

Aspilia kakondensis, sp. nov. *Rhizomate* perenni caules plures ascendentes superne paucirámosos uti folia hirsutos emittente; *foliis* brevipetiolatis oblongo-lanceolatis acutis basi obtusis margine distanter denticulatis trinervibus; *capitulis* ad apicem caulis ramulorumve solitariis pedunculis hirsutis quam folia brevioribus insidentibus; *involucri* campanulati phyllis 2-serialibus exterioribus sursum patentibus oblongo-lanceolatis obtusis basi membranaceis alibi foliosis utrinque hirsutis interioribus quam exteriora brevioribus lanceolatis acutis vel acuminatis omnimodo membranaceis fere glabris; *ligulis* (anne semper?) 8 flavis parum exsertis; *achæniis* (maturis non obviis) oblongo-obovoideis appresse pubescentibus calvis.

Angola, Kakonda, open woods near the barrage of the river Kunene; *Gossweiler*, 2822.

Folia pleraque 4·5–6 × 1·5–2 cm., pag. inf. paullo pallidiora; petioli 5 mm. long. vel minus. Pedunculi 2–3 cm. long. Capitula pansa 13–16 × 15–17 mm.

Involucri phylla ext. usque ad 15 mm. long., ad medium 4 mm. lat., horum pars membranacea 5 mm. long.; phylla int. circa 8 mm. long. Receptaculi paleæ lineari-lanceolatæ, acuminatæ, vix 7 mm. long. Ligulæ late oblongæ, bifidæ, 10 mm. long. Achænia 5 mm. long.

Distinguished on sight from *A. monocephala* Bak. by the relatively broader leaves and the smaller heads with differently shaped involucral leaves. It is also near *A. guineensis* O. Hoffm. & Muschl., which, according to the description in Bull. Soc. Bot. France, lvii. (1910) Mém. 8, p. 116, has, among other features, much larger leaves, outer involucral leaves little more than half as long, and about 12 ligules to the head.

## NOTONIA.

NOTONIA GLAUCA, sp. nov. *Herba* succulenta, procumbens, pruinosa; *foliis* inferioribus —— superioribus sessilibus oblongo-ovatis obtusis basi late amplexicaulibus distanter dentatis vel undulatis nonnunquam breviter lobulatis crassiusculis glaucis eleganter reticulato-venosis; *capitulis* mediocribus ad apicem ramulorum brevium solitariis vel perpaucis; *pedunculis* quam capitula brevioribus uni- vel perpaucibracteatis parvis ovato-lanceolatis acutis; *involucri* campanulati phyllis 13–14 raro adusque 10 reductis oblongis sursum angustatis obtusis apice barbellatis dorso striatulis margine scariosis glaucis; *corollis* aurantiacis exsertis; *achæniis* linearibus apice truncato-dilatatis basi callosis striatis glabris; *pappi* setis corollis brevioribus scabriusculis albis.

Angola, Amibanga de Musende, Libolo; *Gossweiler*, 6439.

Caulis inferne 7 mm. crass. superne 4 mm., optime striatus. Folia summum 7 × 2 cm., superiora sensim minora. Pedunculi ±1 cm. long.; horum bracteæ 6–8 mm. long. Capitula 2 × 1·5 cm. Involucri phylla 16 mm., corollæ 17 mm., achænia 5 mm., pappus 13 mm. long. With its glaucous broadly amplexicaul leaves a very distinct species.

## CRASSOCEPHALUM.

CRASSOCEPHALUM KASSNERI, sp. nov. *Herba* erecta, eramosa vel pauciramosa; *caule* tetragono striato glabro; *foliis* petiolatis ovatis vel ovato-oblongis acutis dentatis vel lobatis vel etiam pinnatifidis tenuiter membranaceis pag. utraque glabris; *capitulis* parvis discoideis 10–12-flosculosis in corymbum elongatum simplicem vel ramosum ordinatis; *involucri* cylindrici phyllis 8–9 lineari-oblongis acutis apice leviter sphacelatis dorso carinulatis glabris; *corollis* exsertis; *styli* ramis breviter appendiculatis; *achæniis* oblongis striatis puberulis; *pappi* setis scabriusculis albis.

Belgian Congo, Musofi, among trees on the mountain slopes; *Kassner*, 2681.

Planta 2–3-spithamea. Folia pinnatifida usque 4–5 cm. long.; horum segmenta ovato-lanceolata dentata 3 cm. long.; folia parva 1·5–2·5 cm. × 5–7 mm.; petioli 5–10 mm., graciles. Corymbi ±25 cm. long.; horum bracteæ inf. pinnatifidæ vel dentatæ, superiores filiformes et ±5 mm. long. Pedunculi proprii tenues, ±5 mm. long. Capitula 7 mm., involucra 4 mm. long. Corollæ tubus 3 mm., limbus 2 mm. long. Achænia 1·25 mm., pappus 3 mm. long.

On a first view this would be sorted to *Senecio* in the neighbourhood of *S. emilioides* Sch. Bip.; but the style-arms are those of *Crassocephalum*. The corolla would appear to have been yellow or possibly mauve.

CRASSOCEPHALUM BUMBENSE, sp. nov. *Herba* perennis circa metralis, patentim ramosa; *ramis* fistulosis eximie costatis puberulis mox glabrescentibus; *foliis* petiolatis ambitu obovatis inferioribus pinnatifidis segmentis ovato-oblongis argute dentatis superioribus ovato-lanceolatis dentatis nonnunquam lobulatis omnibus acuminatis basique in petiolum angustatis membranaceis fere glabris vivis læte virentibus in sicco griseo-viridibus subtus pallidioribus; *capitulis* inter minores discoideis circa 65-flosculosis in corymbum foliis breviorem sat densum digestis; *calyculi* phyllis paucis parvis; *involucri* cylindrici glabri phyllis 13 lineari-oblongis obtusis dorso striatis; *corollis* breviter exsertis; *styli* ramis breviter appendiculatis; *achæniis* oblongis leviter compressis 10-costatis puberulis; *pappi* setis elongatis glabris albis.—*Crassocephalum diversifolium* var. *crepidioides* Hiern, Cat. Welw. pl. iii. p. 595.

Angola, Sobato de Bumba, in moist thickets; *Welwitsch*, 3687.

Folia usque 19×9 cm., pet. 5 cm. long. excluso, superiora pleraque ±10×3 cm., horum petiolus 1–3 cm. long. Corymbi in axillis summis ortis 5–8×2·5–3 cm. Pedunculi proprii graciles, ±4 mm. long. Capitula 11×3 mm. Corollæ croceo-aurantiacæ, 10 mm. long. Achænia 2 mm., pappus 9 mm. long.

The small cylindrical flowering heads serve at once to distinguish this.

Conspecific are Toro, Mpanga Forest; *Bagshawe*, 1010, and Uganda, forest-clearing at Kipayo; *Dümmer*, 1043.

## SENECIO.

SENECIO (§ *Annui*) PAMMICROCEPHALUS, sp. nov. *Herba* sparsim ramosa, circiter bispithamea; *ramis* gracilibus tetragonis striatis glabris; *foliis* parvis suborbicularibus breviter lobatis (lobis obtusis) basi rotundatis vel aperte cordatis pag. utravis glabris petiolis elongatis attenuatis pilosulis fultis; *capitulis* parvulis discoideis circa 12-flosculosis in corymbum laxum elongatum digestis; *involucri* turbinati ecalyculati phyllis 7 lineari-oblongis acutis dorso striatis; *corollis* purpureis exsertis; *styli* ramis truncatis penicillatis; *achæniis* cylindricis glabris; *pappi* setis tenuissimis caducis glabris albis.

Belgian Congo, Mt. Senga; *Kassner*, 2974.

Folia diam. circa 10–12 mm., pag. inf. pallida; petioli 2·5–3·5 cm. long. Corymbus in toto 15–25 cm. long., hujus bracteæ raræ, filiformes, circa 5 mm. long. Capitula fere 3 mm. long. Involucri phylla 2·5 mm. long.

Corollæ tubus 1·75 mm., limbus 1·25 mm. long. Achænia nondum matura ·5 mm., pappus 2 mm. long.

Near *S. emilioides* Sch. Bip., but different in the foliage and much smaller heads.

Senecio (§ *Plantaginei*) ornatus, sp. nov. *Herba* elata, perennis; *caule* erecto simplici striato appresse albo-tomentoso; *foliis* radicalibus inferioribusque elongatis lanceolatis obtusis basi in petiolum longum inferne gradatim dilatatum extenuatis calloso-serrulatis chartaceis utrinque cito glabris vel fere glabris foliis reliquis sensim minoribus sessilibus linearibus obtusis laxe araneosis dein glabrescentibus; *capitulis* majusculis discoideis homogamis ∞-flosculosis in corymbum elongatum pleio- (circa 14-)cephalum tomentosum dispositis; *pedunculis propriis* capitula longe excedentibus; *involucri* campanulati tomentosi phyllis circa 24 oblongis acutis apice sphacelatis; *calyculi* conspicui phyllis erectis linearibus tomentosis; *corollis* dilute luteis vix exsertis; *styli* ramis truncatis penicillatis; *achæniis* oblongis costatis glabris; *pappi* setis scabridis albis.

Angola, Cuanza Norte District, between Quitombe and Camabatela; *Gossweiler*, 7458.

Planta fere 1 m. alt. Caulis circa 5 mm. crass. Folia inferiora circa 22–26 cm. long., juxta medium 3–5 cm. lat., glandulis fuscis immersis obsita; costa media utrobique eminens, lateralibus pluribus ascendentibus, reticulo maxime laxo; petioli 10–15 cm. long. Folia superiora ± 8 cm. long., 3–4 mm. lat., summa in bracteas inflorescentiæ 5–25 mm. long. transeuntia. Corymbus 25 × 10 cm.; pedunculi proprii plerique 4–5 cm. long. Capitula 16 × 15 mm. Involucri phylla 14 mm, calyculi circa 5 mm. long. Corollæ 8 mm., achænia 4 mm., pappus 8 mm. long.

A very distinct and beautiful species, allied apparently, but distantly, to the South African *S. othonnæflorus* DC.

*S. pentecostus* Hiern. Angola, Kintoto; *Gossweiler*, 3810.

*S. Gilgianus* Muschl. in Engl. Bot. Jahrb. xliii. (1909) p. 62, founded on *Eyles* 1239, is identical with Miss Gibbs's 250, previously named by me (Journ. Linn. Soc. xxxvii. (1906) p. 451) *S. barbertonicus* Klatt, var. *microcephala*.

## DICOMA.

Mr. Francis Wilson has recently (Kew Bull. 1923, pp. 377–388) revised this genus. To a large extent his task has consisted in recording the British Museum and Kew Herbarium determinations, a useful undertaking if only to show the richness of both in Cape and South Tropical African material. But he has also proposed alterations in the nomenclature, and rightly so in some cases, though in others exception may be taken to his conclusions. It should be remarked, however, that the delimitation of *Dicoma* species is very difficult, several of them including a number of forms or varieties which some might consider to claim specific rank. Of these varieties Mr. Wilson usually takes no notice, an omission from a formal monograph not worthy of imitation.

He proposes to separate the var. *mirocephala* of *D. anomala* under the name (*D. Gerrardi*) Harvey gave to it in MS., but afterwards withdrew. The heads of this are very small and they have fewer involucral leaves, so that this step may be justified. The Museum sheets have been written up accordingly.

It is impossible to agree with him in regarding *D. membranacea* m. as a synonym for *D. sessiliflora*. The chief differences between the two are shown below, and contrasted with them are characters of what is believed to be a new species related to them. The leaves of all three, it should be noted, are obscurely 3-nerved, a common detail with species which are not 5- (or more) nerved :—

Leaves narrowed at base. Heads about 2×2 cm. Involucral leaves not very pungent, mostly broadly margined.
Leaves coriaceous, five times as long as broa . Heads sessile .... *D. sessiliflora.*
Leaves membranous, three times as long as broad. Heads stalked .......... *D. membranacea*
Leaves broad-based. Heads 3×2·5 cm. Involucral leaves very pungent, only the innermost narrowly margined.
Leaves chartaceous, little more than twice as long as broad. Heads stalked .......... *D. Gossweileri.*

DICOMA GOSSWEILERI, sp. nov. *Herba* perennis, erecta, ⅓ orgyalis ; *caule* valido crebro folioso costato tela alba araneosa circumdato ; *foliis* oblongis obtusis basi breviter amplexicaulibus margine undulatis vel denticulatis chartaceis obscure trinervibus supra mox glabris subtus albo-tomentosis ; *capitulis* homogamis ∞-flosculosis perpaucis (in specimine viso 3) ad apicem caulis breviter pedunculatis pedunculi bracteis lanceolatis spinoso-acuminatis dorso dense araneosis præditis ; *involucri* campanulati phyllis ∞-serialibus lineari-lanceolatis acuminatis maxime pungentibus intermediis quam exteriora (et intima anguste scariosa) plane longioribus omnibus erectis albidis pallideque nitidis ; *flosculis* inclusis ; *corollæ* lobis erectis ; *antherarum* caudis sparsim ciliatis ; *achæniis* dense sericeo-villosis ; *pappi* setis plumosis albis ext. quam int. brevioribus.

Angola, in grassy thickets near Kakonda ; *Gossweiler*, 1752.

Folia usque 8·5 × 3 cm., supra in sicco brunnea, utrinque aperte reticulata. Pedunculi circa 1 cm. long., araneosi ; horum bracteæ circa 2 cm. long. Capitula 3×2·5 cm. Involucri phylla ext. ± 13 mm., intermedia usque 20 mm., intima modo 12 mm. long. Corollæ tubus 4 mm , lobi 7 mm. long. Antherarum caudæ 4 mm., achænia 3 mm., pappi setæ usque 9 mm. long.

Wilson, trusting apparently to the similar heads, places this in *D. quinquefolia*, which has different foliage.

Under *D. nana* Wilson, strangely enough, includes *D. plantaginifolia*, two species with little in common except their acaulescent habit. The latter of these was described by O. Hoffmann (Engl. Bot. Jahrb. xv. (1893) p. 546) on imperfect material, it is true; but, in spite of that, there is no reasonable doubt that Hiern correctly referred Welwitsch's 3615 and 3616 to this species, although the specimens were not altogether satisfactory. Gossweiler's 1207 and 4350 have large mature heads, and these answer Hoffmann's description. The differences between the two can be thus stated:—

| | |
|---|---|
| Leaves broadly elliptical or suborbicular, up to 10 cm. across, 7-nerved. Heads 4×4 cm. | *plantaginifolia.* |
| Leaves obovate, up to 4 cm. across, obscurely 3-nerved. Heads 2·5×2·5 cm. | *nana.* |

Two Rhodesian acaulescent specimens at Kew (Chilanga; *Rogers*, 8528, and Mumbwa; *Mrs. Macauley*, 803), referred by Wilson to the caulescent *quinquenervia*, would seem to belong to an undescribed species near *plantaginifolia*.

In reducing my *D. superba* to *D. quinquenervia* I believe Wilson to be right, but the specimen on which *superba* was founded (*Gossweiler* 1216) on a first view looks very different from the type (at Kew) of *quinquenervia*, it being a strong-growing plant with leaves thrice as wide as those of the other and very large heads. It seems worth a varietal name, and may be called *D. quinquenervia*, var. LATIFOLIA. My var. *angustifolia* of *superba* (Journ. Linn. Soc. Bot. xxxvii. (1906) p. 327) is a remarkable plant: here the narrowed leaves have almost lost their two external nerves, and the heads are much reduced in size. This should be called *D. quinquenervia*, var. ANGUSTIFOLIA. Kassner's 2990 *a* from Mt. Mugila, Belgian Congo, is another variety, or perhaps a form a good deal off type.

*D. vaginata* O. Hoffm. There is no authentic material of this in the London herbaria, but a Museum specimen from the Kilosa subdistrict of the Tanganyika Territory (*Swynnerton* 789) answers the description fairly well. If this be a correct identification, the affinity must be with *D. Kirkii*, not with *D. quinquenervia* as Wilson supposes.

Lastly, a Museum North Cameroons plant (*Talbot* sine no.) is similar to Nigerian specimens (*Dalziel*, etc.) named at Kew and in Wilson's Revision *D. sessiliflora*. The heads, however, are not sessile and there are other differences, *e. g.* the leaves which, although narrow, are 7-nerved at the base. Judging from the description these would seem to be *D. Poggei* O. Hoffm. Swynnerton's 791 from Kilosa, with somewhat broader leaves, is probably conspecific.

## CREPIS.

CREPIS GOSSWEILERI, sp. nov. *Herba* perennis rhizomate crasso sursum circa 1 cm. diam.; *caulibus* erectis compressis optime costatis perpaucifoliosis; *foliis* radicalibus sessilibus obovato-oblongis obtusis basi longe attenuatis margine calloso-denticulatis utrinque præsertim in costis pilis strigillosis appressis inspersis; *capitulis* in paniculam elongatam laxam paucibracteatam oligocephalam digestis; *pedunculis propriis* quam capitula longioribus minute puberulis; *involucri* campanulati phyllis exterioribus parvis anguste linearibus quam interiora 13 linearia obtusiuscula brevioribus omnibus dorso pilis strigillosis nigris vestitis; *receptaculo* plano nudo; *corollis* breviter exsertis; *achæniis* lineari-oblongis compressis in rostrum longum exeuntibus glabris; *pappo* achæniis æquilongo setis glabris albis.

Angola, in woods composed chiefly of *Berlinia Baumii*; *Gossweiler*, 2895.

Planta fere 4-spithamea. Folia pleraque 12–14 cm. long., superne 1·5–2·5 cm. lat. Folia caulina lanceolata, ±4 cm. long. Panicula circa 25 × 12 cm.; bracteæ lineari-setaceæ, ±7 mm. long. Peduncli proprii 1·5–4 cm. long. Capitula 12 × 10 mm. Involucri phylla ext. circa 5 mm., int. 11 mm. long. Achænia 7 mm. long., rostrum solum 2–5 mm. Pappi setæ 6–7 mm. long.

A good deal like *C. polyodon* Bolus, but different in the foliage and somewhat smaller and narrower heads.

## APPENDIX.

In 1913 De Wildemann and Muschler dealt with a number of Kassner's South Tropical African *Compositæ* (Ann. Mus. Congo Belge, sér. 4, ii. pp. 156–180). In several instances the Kassner specimens at the British Museum do not agree with the numbered determinations given by those botanists: the list of discrepancies so far noticed is as below. At the British Museum:—

| | | | | |
|---|---|---|---|---|
| No. 2802 | is | *Berkheya gracilis* O. Hoffm., | not | *Gutenbergia gracilis* Muschl. |
| ,, 2546 | ,, | *Vernonia campicola* S. Moore, | ,, | *V. Calvoana* Hook. f. |
| ,, 3168 | ,, | *V. macrocyanus* O. Hoffm., | ,, | *V. Granti* Oliver. |
| ,, 3005 | ,, | *V. pauciflora* Less., | ,, | *V. Kotschyana* Sch. Bip. |
| ,, 2683 | ,, | *V. musofensis* S. Moore, | ,, | *V. lappoides* O. Hoffm. |
| ,, 3024 | ,, | *V. senegalensis* Less., | ,, | *V. oxyura* O. Hoffm. |
| ,, 2569 | ,, | *V. Petersii* Oliver & Hiern, | ,, | *V. pauciflora* Less. |
| ,, 2711 | ,, | *Gutenbergia Kassneri* S. Moore, | ,, | *V. Smithiana* Less. |
| ,, 2875 | ,, | *Vernonia assimilis* S. Moore, | ,, | *V. zanzibarensis* Less. |
| ,, 2962 | ,, | *Helichrysum Kassneri* S. Moore, | ,, | *H. Buchanani* Engl. |
| ,, 3128 | ,, | *H. fruticosum* Less., | ,, | *H. chrysophorum* S. Moore. |
| ,, 2768 | ,, | *H. Keilii* Moeser (ex descript.), | ,, | *H. leimanthium* Klatt. |
| ,, 3214 | ,, | *H. Newii* Oliver & Hiern, | ,, | *H. Meyeri-Johannis* Engl. |
| ,, 2520 | ,, | *Sphacophyllum candelabrum* O. Hoffm. (reduced form), | not | *Anisopappus africanus* Oliver & Hiern. |
| ,, 2582 | ,, | *Schistostephium heptalobum* Benth. & Hook. f., | not | *S. artemisiæfolium* Bak. |
| ,, 2825 | ,, | *Crassocephalum radiatum* S. Moore, | not | *Senecio purpureus* Linn. |
| ,, 2890 | ,, | *Erythrocephalum caudatum* S. Moore, | not | *E. nutans* Benth. |

No. 2522 named "*Vernonia lavandulifolia* Muschl., in Herb. Berol.," apparently still a *nomen nudum*, is *V. oocephala* Bak., var. *angustifolia* S. Moore (Journ. Bot. lii. (1914) p. 334). Kassner collected this also on Mt. Kundelungu (Nos. 2742 & 2777).

There being already a *Vernonia Kaessneri* (Journ. Bot. xl. (1902) p. 340), No. 2963, described (*op. cit.*) as *V. Kassneri* De Wild. & Muschl., must be renamed. The Museum specimen has a bright grass-green pappus, whereas the one from which the description was made is said to have it a straw-yellow, evidently by a mistake, the pappus having been hastily interpreted as the "green margins" of the upper part of the involucral leaves. The plant may be called V. SMARAGDOPAPPA, comb. nov.

No. 2691 is named "*Athrixia Kassneri* Muschl. in Herb. Berol." It is *Hypericophyllum compositarum* Steetz.

No. 3123, described as *Senecio Dewildemanianus* Muschl., is *S. sycephyllus* S. Moore. Another synonym for this is *S. coreopsoides* Chiov.

For the new species *Senecio parnassiæfolius* De Wild. & Muschl., Kassner's Nos. 2606 and 2994 are cited. The former of these is an *Emilia,* and will consequently be E. PARNASSIÆFOLIA, comb. nov.; the other has been described by me (Journ. Bot. lvii. (1919) p. 119) as *Pseudactis emilioides.*

# Previous Investigations into the Distribution and Ecology of Marine Algæ in Wales. By KENNETH REES, M.Sc. (Communicated by Dr. FLORENCE MOCKERIDGE, F.L.S.)

[Read 23rd April, 1925.]

IN the course of an investigation into the ecology of the Phæophyceæ of the coast of Wales, it was suggested that attention might be paid to the scattered published records of those who, either resident in Wales or visiting its shores, had been gradually building up our present knowledge of its marine flora. The present account, therefore, is an attempt to gather together, from the various sources enumerated in the list of references, material sufficient to compile a chronological account of the development of marine algology in Wales. A list of the seaweeds recorded is retained in manuscript form and is based upon the classification adopted by Batters in his 'Catalogue of British Marine Algæ,' 1902.

## Period 1500–1650.

Though this period may be termed the age of the herbalists it may be noted that, following upon the Renaissance and the re-interpretation of Theophrastus and Dioscorides, attempts were made to arrange, in sections, the plants then known. For marine species the terms "Ulva" and "Fucus" were adopted. In Wales, 'Meddygon Myddfai' with its catalogue of "the names of the herbs, fruits and vegetable substances which every Physician ought to know," was composed and was the basis upon which Dr. John Davies (1570–1644) wrote his 'Botanologium' in 1632 (**9**). References occur in both to "gwimon," "gwig mor," "dylysg y mor," "ysnoden y mor," as Welsh equivalents of Alga or Ulva.

The 'Botanologium' was the forerunner of a number of similar catalogues or lists of plants appearing from time to time in Welsh-English dictionaries (**12, 13, 14, 15**). Of a number of herbals written in Welsh during this period, the most noteworthy is that of William Salesbury (1520–1600) (**46**). Towards the end of the period, Thomas Johnson (d. 1644) a Yorkshireman, who in 1639 visited Wales but recorded no marine plants, published his edition of Gerard's 'Herbal,' in a reprint of which in 1636 (**36**) there occurs a list of Welsh plants sent by Robert Davyes of Guissanay, Flintshire. But neither in this list nor amongst Johnson's marine plants (**37**) is there a definite reference to a seaweed from the coast of Wales.

## Period 1650–1725.

With the publication of How's 'Phytologia Britannica,' in 1650, followed later by Ray (**59**, **60**, **61**), a systematic classification was being attempted and the first reliable records of marine algæ in Wales can be sought. During August 25th–September 7th, 1658, John Ray (1627–1705) made his first itinerary through North Wales (**48**). He touched the coast at Aberconway, Penmaenmawr, Bangor, Menai Bridge, Beaumaris, and Dolgellau. Four years later, during May and June, accompanied by Francis Willughby, the Ornithologist, he made his second itinerary, entering Wales at Wrexham, encountering the sea-board at many places along the north coast, and in Anglesey, as well as at Aberdaron, Pwllheli, Harlech, Aberdovey, Cardigan, Fishguard, St. Davids, Tenby, Laugharne, and Kidwelly, before leaving via Chepstow.

In his diary there are many references to sea-birds, fishes, and maritime flowering plants, but it is only from the internal evidence of his 'Synopsis' (**59**) that conclusions regarding records of marine algæ can be drawn. Of *Padina pavonia* Gaill., he writes "ex insula Anglesey et Cornubiensi"; of *Laminaria digitata* Lam., "Vidimus etiam rupibus marinis aqua pleno mari inundantis copiosissime adnascentum circa Monam insulam" (Note, Vidimus = we saw, *i. e.*, Willughby and Ray). In this work there are several citations of "D. Lhwyd." Edward Lhwyd (1670–1709) explored Wales in 1688 and 1693 to collect in the first instance for the Ashmolean Museum, of which he was Keeper, and in the second for Dr. Gibson's edition of Camden's 'Britannia' (**11**). He also sent many specimens to Ray for his 'Synopsis' and to Dillenius for his third edition of this work. He made further visits in 1826 and later, with Dr. Richard Richardson as companion. In Ray's 'Synopsis' he is credited with *Laminaria saccharina* f. *Phyllitis* Le Jol. and *Fucus spiralis* f. *platycarpus* Thur. Of the former, Lhwyd states: "This in Welsh is called 'Mor Dowys,' the poor people eat the small leaves and clusters as they do 'Delesh' (*Rhodymenia palmata*); the larger are found sometimes two feet long." It is interesting to note that in his 'Archæologia Britannica' (1707), Tit. II., he mentions as examples of "Alga" (Welsh "Gummun," Irish "Duileasg") *Dilsea edulis* Stackh. and *Laminaria digitata* Lam. In Gibson's edition of Camden's 'Britannia' (1695), for which it is so often stated that Lhwyd collected, no marine algæ are mentioned save *Ulva Lactuca* L., concerning the use of which in making "Lhaivan" or "Laver bread" a detailed account is given in the section dealing with St. Davids (**22**, p. 765).

## Period 1725–1760.

This is the period of the pre-Linnean systematists typified by Dillenius in Great Britain. In 1726, during the latter part of May, Littleton Brown (b. 1669) of Bishop's Castle made a short journey through South Wales, of which an account is given in a letter to Dillenius (75, p. lxxiii). He visited the shore at Cardigan, St. Davids, St. Brides, Pembroke and Tenby, but his records are all of flowering plants. However, during a later journey in July 1731, he collected "sea plants . . . . . . some new, especially among the Confervas which came all from Aberystwyth, my journey last July" (75, p. lxxv). Amongst them is *Ahnfeltia plicata* Fries. During late July and throughout August 1726, Dillenius (1684-1747) and Brewer (c. 1700–1742) made a journey into North Wales. Though in the diary of their journey the only reference to marine vegetation is to "two new sea mosses from rocks washed by the sea over against Prestholm I.," it is clear from his herbarium (75) that Dillenius collected many seaweeds during the visit. In all, he records three Blue-Green, eight Green, seven Brown, and twenty-five Red seaweeds, nearly all from Anglesey. Brewer, who remained at Bangor till May 1727, kept a diary of his excursions, but his references to marine algæ are usually of a general character, *e. g.*, in writing of Porthaethwy (Menai Bridge), "I never saw before so grand a variety of Confervas, Corallinæ, and Fucoides as I found in this place, nor so pleasant a sight as the variety of colour and structure in one hole or pool." The pools to which he refers are those on the rocky island of Ynys-y-moch, a name which occurs often in his records of marine algæ. Again, "On the rocks called Trwynhir . . . . . . several curious Confervas, Fucoides, and Corallinæ."

References to particular plants do, however, occur, *e. g.*, "at Trwyn-y-clegin; found in great plenty *Fucus phyllitidis folio* (= *Laminaria saccharina* f. *Phyllitis* Le Jol.), or 'Mor dowys,' and great plenty of a Fucus that is called in N. Wales everywhere 'Dilesh' (*Dilsea edulis* Stackh.) and a great many seedling plants of sea-laces (*Chorda Filum* Stackh.)." But, as in the case of Dillenius, it is from a study of the latter's herbarium that the extent of Brewer's discoveries can be estimated. In his name, two Green, three Brown, and twenty-eight Red seaweeds are recorded, not necessarily different from those of Dillenius himself, twelve being recorded by both (75).

Both in Brewer's diary and in the labelling of the Dillenian herbaria mention is made of Mr. Green, a young clergyman who appears to have resided at Holyhead. He sent many plants to Dillenius (75, pp. lx, lxiii), and accompanied Brewer on some of his excursions. *Himanthalia lorea* Lyngb. and *Ascophyllum nodosum* Le Jol. are recorded in his name. He is mentioned, along with Brewer, as the authority for *Fucus ceranoides* L., *Saccorhiza polyschides* Batt., *Phyllophora membranifolia* J. Ag., *Plumaria elegans* Schm., *Delessaria alata* Lam., and *Ahnfeltia plicata* Fries. Other local botanists mentioned include William Jones, who acted as a guide to Brewer and accompanied Dillenius to Penmon and Llanfaethly, whence three seaweeds are labelled on his authority ; Thomas Price, the conjuror, of whom Brewer writes "he brought me from the weirs he renteth of the Bishop of

Bangor, called Ynys-fadoc-goch, an olive coloured sea garlic, a yellow branched seaweed—it appeared round and tubulous"; and Dr. Foulkes, who not only aided Lhwyd when in North Wales, but sent to Dillenius a number of specimens from his private collection, including the two algæ—*Cystoclonium purpureum* Batt. and *Ceramium rubrum* Ag.

### Period 1760–1824.

In 1753 Linnæus published his 'Species Plantarum,' and for nearly seventy years botanists followed the Linnean system of nomenclature and classification. Amongst the first in Britain was William Hudson (1730–1793), who published his 'Flora Anglica' in 1762. As to whether he visited Wales, information is inadequate. In both Withering's 'Arrangement' (**79**) and Turner and Dillwyn's 'Botanist's Guide' (**74**), plants are recorded for Welsh localities upon the authority of Hudson, who, in his 'Flora Anglica,' either cites Dillenius or Lhwyd, or gives no authority at all for such plants. Only by assuming that these plants quoted without authority are the results of his own observations, may it be suggested that Hudson visited Wales, in which case the visit would be prior to 1762.

In 1773, Rev. John Lightfoot (1735–1788) accompanied by Sir Joseph Banks (1743–1820) visited Wales (**40**, vol. xliii. p. 290). The tour extended from June 25th to August 16th, several weeks being spent in Pembrokeshire. The coast-line was reached at a number of places, *e.g.*, Nash Point, Briton Ferry, Freshwater Bay East, Tenby, Penally, and St. Davids in South Wales; and Abergele, Menai Bridge, Llanddwyn, Llanfaelog, and Cemlyn Bay in North. Maritime flowering plants and ferns are frequently mentioned, but no marine algæ. However, in 'The British Flora' by John Hull (1799), *Alaria esculenta* Grev. is recorded for Holyhead upon the authority of Lightfoot.

Before the next visit, that of John Stackhouse in 1796, there appeared Gough's edition of Camden's 'Britannia' (1789). In a prefatory note the editor writes: "A formal catalogue of plants . . . . . . has, I trust, been in some measure supplied by the help of some young friends who have exerted their utmost diligence in collecting the plants peculiar to each county from books and from the researches of themselves and other botanists who have multiplied since Ray in the same proportion as the Science has improved." The only Welsh county for which marine algæ are recorded is Anglesey:—one Blue-Green, two Green, six Brown, and three Red, of which all, save *Cladostephus spongiosus* Ag. and *Fucus vesiculosus* L., had been previously mentioned by Dillenius or Brewer.

Stackhouse (1742–1819), whose 'Nereis Britannica' appeared in 1801, visited Tenby. Describing *Fucus Opuntia* (= *Catanella repens* Batt.) he writes:—"Specimen hanc rupibus adnascentem juxta Tenby oppidum in Wallia Australi, A.D. 1796 detexi." He also records *Fucus Phyllitis* (= *Laminaria saccharina* f. *Phyllitis* Le Jol.) at the same place.

During the period 1797–1804, a number of pedestrian tours through both North and South Wales were undertaken by persons with a greater interest in history and archæology than in Botany (**1**, **4**, **10**, **19**, **20**, **67**, **76**, **78**). In their diaries or published works, however, a few noteworthy records appear. Rev. John Evans, "accompanied by persons calculated to give assistance to inquiry and stimulus to research," entered upon a journey into Wales in the summer of 1798. At Traethvychan, near Harlech, the appearance of two Cladophoras seems to have attracted his attention. "Swimming like the little Nautilus upon the bosom of the waves appeared *Conferva vagabunda* (=*Cladophora fracta* Kütz.)." "Let the doubting Naturalist watch . . . . the tacking and veering of the vegetable mariner *Conferva Ægagrophila*" (**19**, p. 139). Several references to "Corallines and Fuci" occur in descriptions of a rocky foreshore (**20**, p. 337), but flowering plants form the bulk of his botanical observations. At St. Davids he describes the method of making Llaivan (Laver bread) from *Ulva lactuca* and *Ulva umbilicalis* (=*Porphyra umbilicalis* Kütz.) in words almost identical with those employed in Gibson's Camden's 'Britannia' (**20**, p. 299, *cf.* **22**, p. 765).

Of a similar character was the tour of Arthur Aikin in 1797. Though primarily a mineralogist he frequently gives lists of flowering plants. His references to marine algæ are of a vague and general nature. Writing of Aberystwyth, for instance, he states ;—"Northwards of the castle is a level beach, a few hundred yards in length, to which succeeds a long range of high slate rocks . . . . . . . at the foot of these cliffs extends a reef of low rocks covered at high tide, the crevices and pools of which are adorned with numerous beautiful corallines and fuci" (**1**, p. 47). None, however, are described.

In 1805 appeared Turner and Dillwyn's 'Botanist's Guide.' Marine algæ are recorded for Anglesey (seventeen Fuci, five Ulvæ, ten Confervæ), Carnarvonshire (one Conferva), Denbighshire (two Fuci), Glamorganshire (eleven Fuci, five Ulvæ, ten Confervæ), Pembrokeshire (three Fuci). The authorities quoted are :—Anglesey, Rev. H. Davies and Dillenius ; Carnarvonshire, Dillenius ; Denbighshire, J. W. Griffith ; Glamorganshire, Dillwyn ; and for Pembrokeshire, Dillwyn and Stackhouse. It is somewhat remarkable that Dawson Turner (1775–1858), whose 'Synopsis of the British Fuci' had appeared in 1802, made no reference to those growing on the coast of Wales. In the 'Synopsis' all the Welsh records are upon the authority of Rev. Hugh Davies, except *Fucus palmatus* (=*Rhodymenia palmata* Grev.) and *F. siliquosus* (=*Halidrys siliquosa* Lyngb.), which are mentioned as "common" or "not uncommon" on the shores of England, Wales, and Scotland. Though in the preface to the 'Botanist's Guide' it is stated that Turner was solely responsible for the Cryptogams, in so far as the Welsh counties are concerned, it is mostly for flowering plants that his initials appear as authority. Dillwyn (1778–1855), however, added considerably to our knowledge of the marine algæ, especially of the Swansea district. In his 'British Confervæ' (1809) there are thirty-one Welsh records, mostly upon his own authority. These, together with those found in the 'Botanist's Guide,' in Withering's 'Botanical Arrangement,' and in Gutch's list in the 'Phytologist' (vol. i. p. 184), bring the total number of marine algæ appearing in his name to ten Green, ten Brown, and twenty-three Red species.

Two minor Welsh botanists of this period were William W. Young, who is described by Dillwyn as "an ingenious artist at Swansea," and John Wynne Griffith, of Garn, Denbighshire. Young executed most of Dillwyn's plates for the 'British Confervæ,' and his name appears as authority for seven marine algæ from Newton Nottage, Dunraven Castle, and Laugharne. Griffith, who is mentioned in terms of high praise by Withering in the prefaces to various editions of his 'Botanical Arrangement,' appears as the authority for two Fuci (*Desmarestia ligulata* Lam. and *Dilsea edulis* Stackh.) mentioned for the county of Denbighshire in the 'Botanist's Guide.'

In 1813, Rev. Hugh Davies (1739–1821) published 'A Welsh Botanology,' a comprehensive flora of Anglesey, containing an excellent list of algæ under the headings "Fucus" (fifty-eight, all marine), "Ulva" (twenty-five, of which twenty-one are marine), and "Conferva" (eighty-six, of which forty-two are marine). An analysis of this list and of references to Davies in contemporary algal literature (**17**, **24**, **26**, **33**, **42**, **70**, **73**, **74**, **79**), brings the total of his records to two Blue-Green, eighteen Green, thirty-two Brown, and fifty-eight Red species. He appears to have been frequently consulted by Turner, Goodenough, and Woodward, upon critical species or points of nomenclature.

## Period 1824–1878.

With the publication in 1824 of C. Agardh's 'Species Algarum,' the natural system, as the basis of classification, was extended to marine algæ. When therefore, John Ralfs, of Penzance, visited Wales in 1841, a new nomenclature was in force and the algæ he recorded can be identified with greater accuracy than is possible in the case of previous investigators. Ralfs visited Wales again in 1842 and several subsequent years, and in 1842 was accompanied by William Borrer, a Sussex algologist. In all, he recorded eight Blue-Green, seven Green, nine Brown, and twenty-two Red seaweeds (**26**, **55**, vol. i. pp. 193, 490, and 184). Ralfs was the first botanist, who had made algology a life-study, to visit Wales, and his records amongst the smaller species are of considerable interest. His journeys, too, extended over a wide area, the coastline from Swansea, the Gower and Milford Haven in the south, through Aberystwyth, Barmouth, and Dolgellau in Cardigan Bay, to Carnarvon, Bangor, Menai Bridge, Holyhead, and Aberffraw in the north, being carefully explored.

Both Harvey (**26**) and Ralfs mention Rev. T. Salwey, of Oswestry. He recorded *Taonia atomaria* J. Ag. at Tenby, and *Nodularia spumigena* f. *litorea* Born. & Flah. at Barmouth, at a date prior to 1843.

In 1844, J. W. G. Gutch, of Swansea, contributed to 'The Phytologist' (vol. i. p. 184) a list of plants in the neighbourhood of Swansea. The list includes a catalogue of marine algæ. Apart from two citations of Ralfs and a repetition of Dillwyn's records in the 'Botanist's Guide,' the list appears to be the result of Gutch's own observations, which total eleven Green, fourteen Brown, and forty Red species.

A local list of the same character is that of Thomas Owen Morgan of Aberystwyth. In 'Flora Ceretica Superioris' (1849), under the heading Algæ, he writes:—"The rocks extending from the beach at Aberystwyth towards the west are covered every tide at high water, but at low water become exposed to view and form pools and crevices which furnish the collector with a variety of algæ and corallines for preserving. The following list of marine plants found there may, for that purpose, prove useful." The list comprises five Green, twenty-three Brown, and twenty-eight Red seaweeds. As the list includes *Himanthalia lorea* Lyngb., *Saccorhiza polyschides* Batt., *Sporochnus pedunculatus* Ag., and *Dictyopteris membranacea* Batt., none of which are found there to-day, one may conclude that either a remarkable change has taken place in the local marine flora or that Morgan's observations did not err on the side of accuracy. Morgan also produced a 'Guide to Aberystwyth' with a list of flowering plants, an example followed by several later compilers of "Guides" (**7, 35, 38, 51, 64**). None, however, contain lists of marine algæ.

## Period 1878–1920.

The studies of Bornet and Thuret on sexual fertilization (1878) may be said to mark the beginnings of modern marine algology. Algologists turned their attention from mere collecting for herbaria to a critical study of marine species, their morphology, cytology and, more recently, their ecology and physiology. One effect of this has been to limit records to a few species or families in which the observer was interested. Thus Dr. J. E. Gray, in a note on *Desmarestia* (**40**, vol. iii. p. 171) writes:—"In Wales I have found these two plants (*D. ligulata* Lam. and *D. viridis* Lam.) growing apparently from the same root disc." This was probably in 1865. In April 1881, E. M. Holmes visited North Wales and found *Phlœospora subarticulata* (= *Stictyosiphon subarticulatus* Hauck) at Carnarvon (**21**, vol. ii. p. 142). Either then or during a later visit he recorded several other species in Anglesey or Menai Strait (**25**, **40**, vol. lii. p. 250), and at a meeting of the Linnean Society in March 1911 exhibited *Griffithsia globifer* J. Ag. from Milford Haven. In 1885, during the latter part of June, Dr. O. Nordstedt visited Wales and recorded *Symploca atlantica* Gom. at Ferryside, Carmarthenshire (**21**, vol. xxii. pp. 22 & 51), and *Vaucheria litorea* Bang. et Ag. between Dolgellau and Barmouth (**66**, p. 382). In 1886 (**21**, vol. xv.) and 1890 (**21**, vol. xxii. p. 91) E. A. L. Batters came to North Wales, and, judging by records in his 'Catalogue of the British Marine Algæ' (1902), he botanised chiefly at Point of Ayr (Flintshire) and Puffin Island, though, in addition, there are records for Rhyl, Bangor, and Holyhead. He added eight Blue-Green, six Green, five Brown, and six Red species to those previously recorded.

In 1914, A. D. Cotton, studying the ecology of *Ptilota plumosa* Ag., *Callithamnion arbuscula* Lyngb., and *Codium mucronatum* f. *atlanticum*, visited Barmouth, Aberystwyth, Fishguard, Strumble Head, Newport, and Dinas Bay. He failed to find these three species, but notes the *Nemalion* and *Callithamnion* associations at Dinas Bay and *Porphyra* association at Newport (**40**, vol. lii. p. 35).

In addition to these somewhat scattered records, there appeared during the last decade of the 19th century three notable contributions towards a complete list of marine algæ for the coasts of Anglesey and Carnarvonshire. The first was that of R. J. Harvey-Gibson. In the 'Proceedings of the Liverpool Biological Society,' vol. iii. (1889) and in Report III. of the Liverpool Marine Biological Station (1892), he published lists of marine algæ for many areas including Anglesey and Puffin Island. In all, fifteen Blue-Green, thirty-two Green, fifty-six Brown, and ninety-four Red seaweeds are recorded.

The second appeared in 1895 in John E. Griffith's 'Flora of Anglesey and Carnarvonshire,' and contained seven Blue-Green, twenty-two Green, forty-three Brown, and ninety-nine Red species. Lastly, in 1896, Professor R. W. Phillips published a list of sixty-one Brown seaweeds (**54**) gathered, like those of Griffith, from many localities in the Menai Strait and Anglesey.

Since that date, apart from a very incomplete list for Aberystwyth (**69**), there has been no further contribution to our knowledge of the distribution of marine algæ on the coast of Wales.

The records of the investigators whose activities have been described are brought together in a manuscript list, which comprises thirty Cyanophyceæ, forty-eight Chlorophyceæ, eighty-five Phæophyceæ, and one hundred and thirty-eight Rhodophyceæ, a total of three hundred and one species, confined, however, very largely to four coastal areas:—Anglesey (including Menai Strait), Aberystwyth, Pembrokeshire, and the Gower.

In conclusion I would wish to express my thanks to both Prof. R. W. Phillips of Bangor and Prof. J. Lloyd Williams of Aberystwyth for their kindness in allowing me to read private copies of books and manuscripts, and to the latter for many helpful suggestions and criticisms.

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# A Critical Study of certain Species of the Genus *Neuropteris* Brongn.

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(PLATES **5** & **6**, and 5 Text-figures.)

[Read 5th November, 1925.]

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## 1. INTRODUCTION.

EARLY in 1920 the writer, whilst working on the Coal-Measure Plants of the Northumberland and Durham Coalfield, collected material from a band of ironstone nodules occurring in brick clays at the Phœnix Brick Works, Crawcrook, Co. Durham. The nodules proved to be rich in plant-remains, and particularly in species of the genus *Neuropteris*. The identification of these specimens proved difficult, owing to the large numbers of specimens apparently intermediate between recorded species. The frequency with which these intermediates occurred suggested that they were stable forms, quite as much so as the usually accepted species. This discovery of what clearly seemed to be stable intermediates between types accepted hitherto as species led me to investigate more closely the whole question of what forms owed their supposed specific characters to the position they occupied upon the rachis or to conditions of development.

Subsequent research has shown that *Neuropteris* intermediates occur throughout the coalfields of England.

This paper contains the results of investigations into the question of what forms may be retained as valid species and what as intermediates. The character and development of the different modes of pinnule growth in different parts of the frond are also considered.

## 2. Remarks on the Genus *Neuropteris*.

1822. *Filicites* (Section *Neuropteris*) Brongniart, Classification des Végétaux fossiles, p. 33.
1826. *Neuropteris* Sternberg, Essai flore du monde primitif, vol. i. fasc. iv. p. 16.
1828. —— Brongniart, Prodrôme, p. 52.
1886. —— Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 249.

### *Diagnosis of* Neuropteris. (Brongn., **5**, p. 226.)

"Folia bipinnata, vel rarius pinnata, pinnulis basi sæpius subcordatis, nec inter se nec rachi integrâ adnatis, sed parte mediâ tantùm insertis; nervo medio apice evanescente; nervulis obliquis arcuatis tenuissimis dichotomis."

Members of this genus were large plants bearing enormous fern-like fronds, some of which bore seeds (Kidston, in Phil. Trans. Roy. Soc. Edin. vol. cxcvii. (1904) pp. 1–5), a fact which at once clearly separates them from true Ferns. "The fronds were probably tripinnate as well as bipinnate. The principal rachis bifurcated at a more or less wide angle, and the pinnæ arising near the angles of bifurcation were much less developed and less cut up than were the external pinnæ, being often only simply pinnate when the latter were bipinnate. There was therefore a notable disparity between the two sides on the same portion of the rachis" (Zeiller, **20**, p. 249).

The *Neuropteris* pinnule, with few exceptions, has the margin entire, and the surface of the lamina smooth, except *N. Scheuchzeri* Hoffm., where the surface is covered with fine hairs. The apex varies from round to acute, and the venation, except in *N. rarinervis* Bunbury, does not vary much in density. The amount of overlap of the pinnules varies much, being influenced partly by environment and partly by fossilisation.

### *Validity of certain Species.*

That some of the earlier workers were doubtful as to the validity of certain species is evident from their writings. Brongniart (**5**, p. 237) even expressed doubt about the validity of some of his own species. Bunbury says: "I must observe that the number of described species is probably far too great, and that the greater proportion of them would probably be found, if completely known, to be variations or modifications of a few real 'specific' types. Many of them have been described from very imperfect specimens, often, indeed, mere fragments. Now, in those kinds of *Neuropteris* which are best known we see that (as in many ferns) the size, outline, and position of the leaflets vary very much in different parts of the same frond. . . . In making use, therefore, of such imperfect material as we most often have before us, in the case of fossil plants, we are exceedingly liable to create false species, and to describe under several distinct names different fragments which may even have originally grown from one root." This statement of Bunbury has in a large measure proved to be correct.

### 3. Diagnostic Characters.

Early in this enquiry it soon become evident that it was necessary to determine what features could be considered as constituting adequate diagnostic characters.

Kidston and Zeiller regarded the number of veins entering a centimetre of leaf-margin as a satisfactory diagnostic character. The result of the actual count of veins per centimetre by us, counted on a large number of specimens, shows that there is not sufficient constancy of veins per centimetre to make this of any great value. The reason for this inconsistency is that no new veins are produced by a leaf after its development in the bud; the only growth which takes place is in the lamina itself, which expands as a result of growth of the tissues between the veins. As a result of this growth the veins become farther apart; consequently the number of veins entering the margin in a mature leaf is less than those entering the same area in an immature leaf. Therefore it is not possible to employ the number of veins entering a centimetre of leaf-margin as a diagnostic character, unless the leaves be of the same age. Both Kidston and Zeiller made use of this as a diagnostic character, and it has led to a certain amount of confusion between the species. Owing to the failure of this diagnostic character there remain those of size and shape. Very few of the earlier writers realized the fact that the sizes of the pinnæ and pinnules are dependent to a large extent on their age and position on the plant. Consequently a number of specimens closely resembling certain species in everything but size have not been referred to these species by Brongniart and other authors, solely because of size-difference (Zeiller, **20**, p. 277).

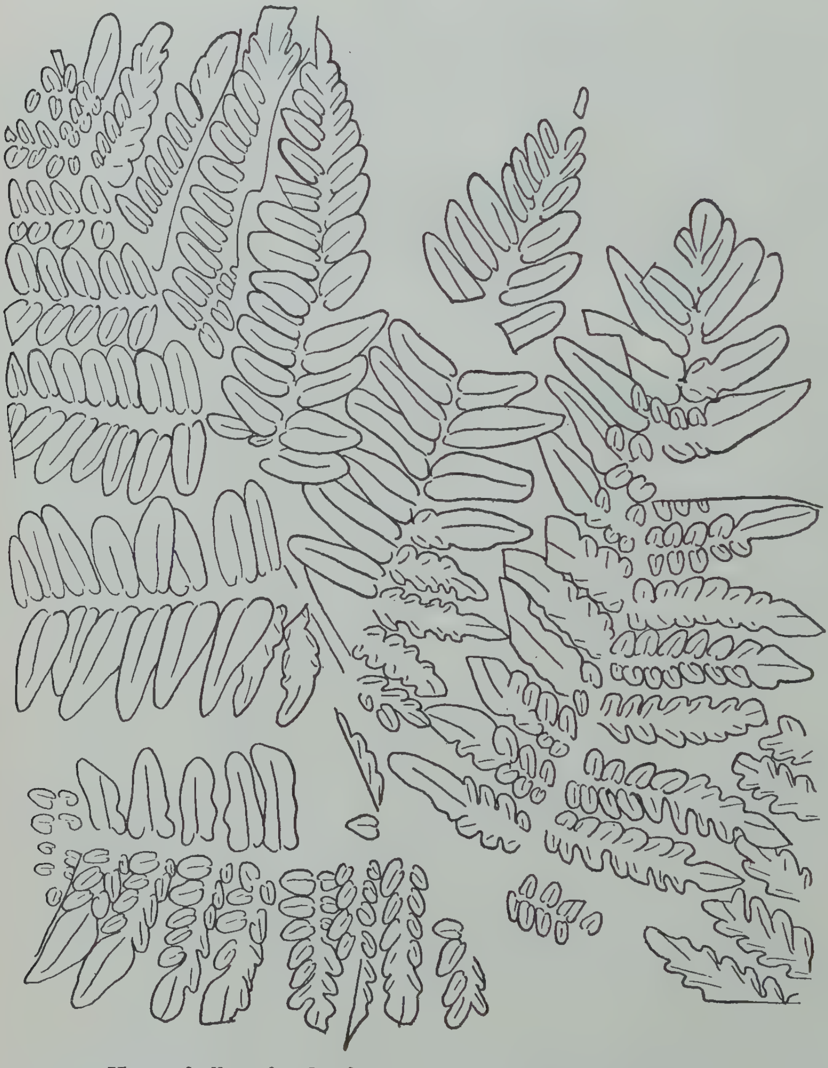
Since internal structure is not available for study, specific differences must, for the present, be founded entirely on external characters. As these are to a large extent influenced by environment, age, and position on the plant, all these factors must be taken into account when identifying specimens of *Neuropteris*.

That *Neuropteris* fronds were not always homophyllous but were also frequently heterophyllous is evident when large portions of fronds are found. A good example is seen on the specimen figured by Zeiller (**20**, p. 43), a tracing of which is given in text-fig. 1.

Many of these heterophyllous forms are, I am certain, to be found amongst specimens now identified as *N. heterophylla* Brongn. There is abundant evidence, as will be seen later, that *N. heterophylla* Brongn. has become a somewhat "omnibus" species, to which is relegated quite a number of variants and intermediates of other species.

The determination of the mode of development of pinnules and their probable position on the frond has formed the chief basis of determination of specific character in this paper. Thus, in identifying a specimen of *Neuropteris*, it was first necessary to consider its probable age (whether immature or fully grown), its relation to the rest of the pinna, and the probable relation of that pinna to the frond. It is only by a careful consideration of these factors that a specimen can be correctly identified.

Fig. 1.



Heterophyllous fronds of *Neuropteris*, after Zeiller (reduced).

By adopting the above methods, we are now in a position to restate the characters of most of the common British Coal-Measure species of *Neuropteris*, and to indicate more clearly the detailed features of frond development. It will be further shown that it is possible for the known species of *Neuropteris* to be brought together into "species-groups" (Gregory, 8, p. 22). These species-groups will now be described in detail.

### 4 A. **Species-group** N. FLEXUOSA.

NEUROPTERIS FLEXUOSA Sternb.

1823. *Neuropteris flexuosa* Sternberg, Flora der Vorwelt, Vers. i. fasc. IV. p. 16; Vers. ii. p. 71.

1826. *Neuropteris ovata* Hoffmann, in Keferstein's Teutschland geognostisch-geologisch dargestellt, vol. iv. p. 158, pl. 1 *b*. figs. 5–7.

1830. *Neuropteris flexuosa* Brongniart, Histoire des Végétaux fossiles, p. 239, pl. 68. fig. 2; pl. 65. figs. 2, 3.

1847. —— —— Bunbury, in Quart. Journ. Geol. Soc. London, vol. iii. (1847), p. 425; vol. xiv. (1858), p. 248.

1869. —— —— Schimper, Traité de Paléontologie Végétale, vol. i. p. 434, pl. 30. figs. 12, 13.

1876. —— —— Heer, Primæval World of Switzerland, vol. i. p. 10.

1886. —— —— Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 277, pl. 46. fig. 2.

1823. *Neuropteris plicata* Sternberg, Flora der Vorwelt, Vers. i. fasc. IV. p. 16; Vers. ii. p. 74, pl. 19. figs. 1 & 2.

1830. —— —— Brongniart, Histoire des Végétaux fossiles, p. 248.

1859. *Neuropteris rotundifolia* Bunbury, in Quart. Journ. Geol. Soc. London, vol. xiv. (1858), p. 248.

1823. *Osmunda gigantea* var. $\beta$, Sternberg, Flora der Vorwelt, Vers. i. pp. 36, 39, pl. 32. fig. 2.

1830. *Neuropteris heterophylla* (in part) Brongniart, Histoire des Végétaux fossiles, p. 243.

1886. —— —— Zeiller, Flore fossile du Bassin houiller de Valenciennes, pls. 43, 44, p. 361.

1830. *Neuropteris Loshii* Brongniart, Histoire des Végétaux fossiles, p. 242, pl. 62. fig. 1, pl. 63.

1830. *Neuropteris Soretii* Brongniart, *ibid.* p. 244, pl. 70. fig. 2.

1823. *Neuropteris thymifolia* Sternberg, Flora der Vorwelt, Vers. ii. p. 75.

1830. *Neuropteris microphylla* Brongniart, Histoire des Végétaux fossiles, p. 244, pl. 74. fig. 6.

1887. *Neuropteris ovata* Kidston, in Proc. Roy. Soc. Edin. vol. xxxiii. pt. ii. (1887), p. 359, pl. 22. fig. 1.

#### *Remarks on synonymy of* NEUROPTERIS FLEXUOSA *Sternb.*

N. FLEXUOSA.

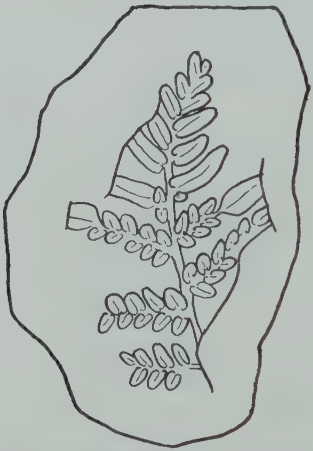
Careful examination of a large number of specimens in various collections has proved that a number of immature specimens of *N. flexuosa* Sternb. were grouped with other species under the specific name *N. heterophylla* Brongn. Brongniart himself (5, p. 243) states that it is difficult to distinguish some forms of *N. heterophylla* Brongn. from other well-known species. This difficulty was probably due to the fact that earlier authors did not make sufficient allowance for growth changes. For instance, Zeiller

(20, p. 277) says that *N. flexuosa* Sternb., although closely resembling certain forms of *N. heterophylla* Brongn., is distinguished from it by the fact that it is never found so small. He failed to realise that his *N. flexuosa* pinnæ might be but the mature stage, and certain forms of *N. heterophylla* he mentions, the smaller immature stage of one and the same species.

NEUROPTERIS LOSHII.

The specimens figured by Brongniart (5, pl. 72. fig. 1 & pl. 73) of which pl. 72. fig. 1 is reproduced as text-fig. 2, under the name *Neuropteris Loshii* Brongn., are clearly only the immature forms of *N. flexuosa* Sternb. The type-specimens of this species (*N. Loshii* Brongn.) came from the Newcastle Coalfield, an area in which *N. flexuosa* Sternb. is very common, and these two species are frequently found in close association. Brongniart further remarks upon the resemblance between *N. Loshii* Brongn., *N. tenuifolia* Schloth. (sp.), and *N. flexuosa* Sternb., but suggests that the chief difference lies in the size, character of venation (being thicker and more compact in *N. Loshii* Brongn.), and also in the less caducous nature of the pinnules of *N. Loshii* Brongn. These are all characters which are, to a great extent, governed by age, growth, and position on the rachis.

FIG. 2.



*Neuropteris Loshii* after Brongniart (reduced).

Bunbury (7, p. 248) says that after careful examination of a great number of specimens, he is unable to satisfy himself, owing to the occurrence of intermediate forms, that *N. flexuosa* Sternb. is permanently distinct from *N. gigantea* Sternb. He also considers that the overlapping of the pinnules in the former species, a character on which Brongniart lays great stress, is not to be relied on. My observations are in agreement with Bunbury. Heer (9, p. 10) suggests that such forms as *N. gigantea* Sternb. and *N. Liberti* Heer are nearly allied to *N. flexuosa* Sternb.

NEUROPTERIS ROTUNDIFOLIA.

Brongniart (**5**, p. 238), in giving specific rank to the form of *Neuropteris* pinnule known as *N. rotundifolia*, expresses doubt as to its specific distinctness from *N. flexuosa* Sternb. Bunbury (**7**, p. 248), when speaking of this species, says: "I cannot but believe this to be a mere variety of *N. flexuosa* Sternb., as I have seen on the very same fragments leaflets corresponding with the characters of both."

N. HETEROPHYLLA.

A close study of the figures and description published by Zeiller (**20**, p. 261, pls. 43, 44) of *N. heterophylla* Brongn. shows that the specimen he figures are portions of large fronds of the *N. flexuosa* Sternb. type, showing its heterophyllous character.

These illustrations (see text-fig. 1, p. 298) have considerable value and interest, as they show pinnæ having the characters of *N. heterophylla* Brongn. and *N. flexuosa* Sternb., together with intermediates, all borne on the same rachis. An indication of so clear a character of the actual occurrence of two supposed species types upon the one rachis, and also in association with intermediates, can hardly be set aside.

*Neuropteris* fronds are rarely obtained in large masses, and the opportunity of surveying the whole or a large portion of a whole frond does not often occur, and therefore few comparisons between pinnæ in various positions can be obtained. In the case just cited, the lowest pinna in the left-hand corner of the specimen figured (text-fig. 1, p. 298) is of particular interest, as it shows two kinds of lateral pinnæ occurring on opposite sides of the same rachis. Only single, large, and simple pinnules are found on the upper side of the rachis, whilst on the lower side small pinnæ occur, having the apical pinnule of the same size and shape as the simple pinnules found on the other side. The late Dr. E. A. N. Arber (**1**, p. 171) was the first worker to point out this dimorphic character, which he found in a specimen identified by him as *N. obliqua* Brongn. The great caducity of the pinnules may perhaps be the reason why so few of these dimorphic fronds are found.

Lindley and Hutton (**15**, p. 183) figured one of these dimorphic pinnæ, which they identified as *N. heterophylla* Brongn.

Dr. E. A. N. Arber (**2**, p. 33) figures a single pinna, and refers it to *N. heterophylla* Brongn. In the light of knowledge gained from a study of a large number of specimens, I identify the pinna as referable to *N. flexuosa* Sternb. The pinnules are certainly more rotund than is the case in normal forms of *N. flexuosa* Sternb., thus approaching the varietal form of *N. flexuosa* Sternb. known as *N. rotundifolia* Brongn.

It is of interest to note how many of the same authors who have described and identified *Neuropteris* fronds compared them with *N. flexuosa* Sternb., as if this species represented the genus type of the *Neuropteris* frond.

NEUROPTERIS SORETII; N. MICROPHYLLA; N. THYMIFOLIA.

*N. Soretii* Brongn., *N. microphylla* Brongn., and *N. thymifolia* Sternb. are youthful forms of species belonging to the "species-group" of which *N. flexuosa* Sternb. is the type and most probably to *N. flexuosa* Sternb. itself. The only differences occurring among these species are those governed by age and position, such as size, compactness of venation, etc. In comparing *N. microphylla* Brongn. with *N. flexuosa* Sternb., Brongniart (**5**, p. 245) says: "With the exception of the great difference in size, one would consider it to be the same plant." And Schimper (**18**, vol. i. p. 441) is of the same opinion. He also suggests uniting *N. Loshii* Brongn., *N. tenuifolia* Schloth. (sp.), and *N. Soretii* Brongn. with *N. flexuosa* Sternb., as he possessed specimens of these species which appeared to be intermediates.

N. PLICATA.

Dr. Kidston (**14**, p. 95) placed *N. plicata* Sternb. with *N. flexuosa* Sternb., as he was unable to find any point by which they could be separated, but later (Trans. Roy. Soc. Edin. vol. xxxv. (1889), pt. 5, p. 313) he decided that the true *N. plicata* Sternb. was not a variety of *N. flexuosa*. Specimens of this species are very rare, and I have not seen one.

N. OVATA.

The description given by Dr. Kidston (**10**, p. 360) of Hoffmann's species states that "the terminal pinnule in *Neuropteris ovata* Hoffm. is never enlarged as in *N. flexuosa* Sternb. It is usually more or less broadly lanceolate, and at its basal extremity is connected with the uppermost pinnule or pinnules. The pinnules are auricled in a manner similar to those of *N. flexuosa* Sternb., but they do not overlap so much as in the latter-mentioned species. The veins are more arched than in *N. flexuosa* Sternb., and also appear more numerous." All the distinguishing characters, as given by Dr. Kidston, between these two species are such as are entirely dependent on age and position on the rachis. Again, *N. ovata* Hoffm. differs so slightly from some forms of *N. Loshii* Brongn. that a close relation between the two seems inevitable.

### *Revised diagnosis of* NEUROPTERIS FLEXUOSA *Sternb.*

Frond dimorphic, containing both major and minor pinnules. Minor pinnules varying in size up to 1·5 cm. in length and 1 cm. in width, elongate-oval or oval, occasionally rotund, attached to the axis by a small part of the base. Apical pinnule very large, with the greatest width usually occurring just below the middle of the pinnule. Lateral veins very clear, medium thickness, not much arched, dichotomising two or three times. Median vein clear, running up about three-quarters of the pinnule, then dividing up into smaller veins. Major pinnules large, generally similar in shape and size to the apical pinnules of the minor pinnæ. Attached to the rachis by a small part of the base. Venation as in minor pinnules.

### *Distribution.*

*N. flexuosa* Sternb. is common throughout the Coal Measures of Great Britain, but particularly in the Middle Coal Measures, as also are its intermediate forms.

## NEUROPTERIS GIGANTEA Sternb.

1820. *Filicites linguaris* Schlotheim, Die Petrefactenkunde, p. 411.
1823. *Osmunda gigantea* Sternberg, Essai d'un Exposé geognostico-botanique de la flore du monde primitif, vol. i. fasc. II. p. 32, pl. 22.
1826. *Neuropteris gigantea* Sternberg, *ibid.* fasc. IV. p. 16.
1830. —— —— Brongniart, Histoire des Végétaux fossiles, p. 240, pl. 69.
1832. —— —— Lindley & Hutton, Fossil Flora, vol. i. pl. 52.
1848. —— —— Sauveur, Végétaux fossiles des terrains houillers de la Belgique (Académie royale des sciences de Belgique), Bruxelles, pl. 33. fig. 1.
1848. *Neuropteris flexuosa* Sauveur (*non* Sternberg), *ibid.* pl. 32. figs. 91, 92.
1886. *Neuropteris gigantea* Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 258, pl. 42. fig. 1.
1892. —— —— Potonié, Ueber einige Carbonfarne, iii. Theil, p. 22, text-figs. 1–4, pl. 2. figs. 1–2; pl. 3. figs. 1–4; pl. 4. figs. 1–2 (Jahrb. d. K.-Preuss. Geol. Landesanstalt, 1891).
1892. *Neuropteris Zeilleri* Potonié, Ueber einige Carbonfarne, iii. Theil, pp. 22, 32, fig. 105. Id., Lehrb. d. Pflanzenpal. p. 113, fig. 101; p. 118, fig. 105; p. 153, fig. 150.
1899. —— —— Hoffmann & Ryba (part), Leitpflanzen, p. 64, pl. 9. figs. 4, 4 *a*, 4 *d* (not pl. 8. fig. 14; pl. 9. fig. 3).
1899. —— —— Zeiller, Flore fossile du Bassin houiller d'Heraclée, p. 44, pl. 4. fig. 10.
1899. *Neuropteris pseudogigantea* Potonié, Lehrb. d. Pflanzenpal. p. 113, fig. 102.
1900. *Neuropteris gigantea* Zeiller, Éléments de Paléontologie, p. 105, fig. 79.
1901. —— —— Kidston, in Proc. Yorks. Geol. & Polytech. Soc. vol. xiv. (1901), pp. 193, 211, 213, pl. 28. fig. 5; pl. 29. fig. 4.

### *Remarks on synonymy of* N. GIGANTEA *Sternb.*

Sternberg is extremely vague in his description of this species published in 1823; all he says is that as the venation is very similar to that of the recent genus *Osmunda*, and is also the largest known form, he proposes to call it *Osmunda gigantea*. Fortunately his figure of the specimen which came from Schatzlar is clearer than his description. In the same work he figured a specimen which he states "appears to be a species or variety of *Osmunda gigantea*." This supposed varietal form has, however, characters which are intermediate between those assigned to *N. flexuosa* Sternb. and *N. tenuifolia* Schloth. (sp.).

### N. FLEXUOSA.

*N. gigantea* Sternb. is linked up with *N. flexuosa* Sternb. by a number of intermediates. In the absence of the terminal pinnule, it is frequently difficult to distinguish between the pinnæ of the two species, so close is the resemblance between them. In fact, Bunbury (**6**, p. 45), in describing some intermediate forms, expresses doubt as to whether *N. flexuosa* Sternb. and *N. gigantea* Sternb. are specifically distinct. Brongniart (**5**, p. 240), in noting the resemblance between *N. flexuosa* Sternb. and *N. gigantea* Sternb., states that the pinnules are longer and narrower in *N. gigantea* Sternb. I do not agree with this statement, as I have seen specimens of *N. flexuosa* Sternb. in which the pinnules show a close approximation in these features to *N. gigantea* Sternb.

### NEUROPTERIS GRANGERI.

Schimper (**18**, p. 441) expresses the view that *N. Grangeri* Brongn. is intermediate between *N. flexuosa* Sternb. and *N. gigantea* Sternb. Brongniart (**5**, p. 237), whilst separating *N. Grangeri* from *N. gigantea*, considers that the differences may be due to the positions which the plant fragments occupied on the one rachis.

### N. CISTII.

Brongniart is similarly in doubt of the existence of a true specific distinction between his own species *N. Cistii* and *N. Grangeri*. My own studies have confirmed this view. In some cases pinnules having the characters of *N. tenuifolia* Schloth. (sp.) occur on pinnæ which are undoubtedly specimens of *N. gigantea* Sternb. Pinnules of this character are shown to occur even on the figure of the type-specimens (text-fig. 3).

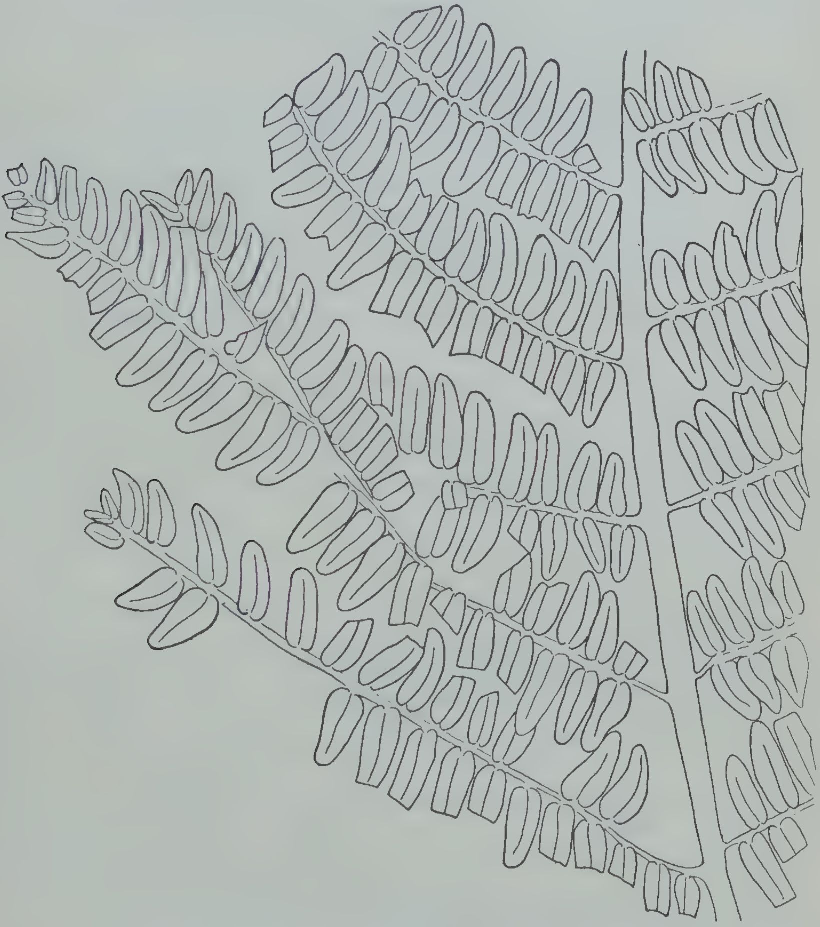
I have seen several specimens showing both types of pinnule on the same plant. This evidence seems to be conclusive as to the identity of one form with the other.

### *Diagnosis of* NEUROPTERIS GIGANTEA *Sternb.*

*N.* foliis bipinnatis, pinnis patentibus elongatis, pinnulis vix contiguis (nec imbricatis) oblongis obtusis, basi rotundatis (nec dilatato-cordatis); nervulis tenuissimis approximatis arcuatis dichotomis; nervo medio vix distincto evanescente.

Brongniart published this diagnosis of Sternberg's species in 1830 (**5**, p. 240), as that author gave an illustration only. Zeiller (**20**, p. 42) gives a very full description of the species, and therefore I include it here:— "Fronds very large, tripinnate, secondary rachis 5–12 mm. wide, marked with longitudinal striation, also with irregular punctations corresponding without doubt to scales, and having orbicular or oval pinnules between the secondary pinnæ, which are contiguous or else overlapping. Primary pinnæ 20–30 cm. apart, slightly overlapping, 20–35 cm. wide, and not less than 80–100 cm. long, remaining the same size for a large part of their length, but becoming smaller towards the top. Secondary pinnæ alternate, or subopposite, straight or slightly arched, 2–5 cm. apart, contiguous or, what is more usual, overlapping, 25–55 mm. wide, 12–20 mm. long. Narrow, oval, lanceolate in shape, contracted at the top to an obtuse apex. Pinnules sub-opposite or alternate, sessile, easily detached, straight, 10–25 mm. long, 4–10 mm. wide, contiguous or overlapping. Heart-shaped at the base, margins parallel, rounded at apex, diminishing somewhat in length towards apex of secondary pinnæ. Terminal pinnule oval, smaller than the rest.

Fig. 3.



Reduced from figure of type-specimen of *Neuropteris gigantea.*

The pinnules attached directly to the rachis are either orbicular, oval, or triangular with rounded angles, 5–15 mm. long, 3–12 mm. wide. Median vein marked by a slight groove, dividing a little beyond the middle of the pinnule, arched, frequently dichotomising into numerous compact and fine veins. The cyclopteroid pinnules are frequently devoid of a median vein, the veins radiating out from the point of attachment."

*Distribution.*

*N. gigantea* occurs throughout the British Coal Measures. It is not very common in the Lower Coal Measures, its maximum development being reached in the Transition and Upper Coal-Measure Series.

### NEUROPTERIS TENUIFOLIA Schloth. (sp.).

1820. *Filicites tenuifolius* Schlotheim, Die Petrefactenkunde, p. 405, pl. 22. fig. 1.
1826. *Neuropteris tenuifolia* Sternberg, Flora der Vorwelt, Vers. i. fasc. IV. p. 17; Vers. xi. fasc. V.–VI. p. 72.
1828. —— —— Brongniart, Prodrôme, p. 53.
1830. —— —— Brongniart, Histoire des Végétaux fossiles, p. 241, pl. 72. fig. 3.
1852. —— —— Bronn, Lethæa Geognostica, vol. i. pl. 11, p. 110; pl. 7. fig. 4 *a*, *b*.
1869. —— —— Schimper, Traité de Paléontologie, p. 438.
1886. —— —— Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 273, pl. 46. fig. 1.
1848. *Neuropteris gigantea* Sauveur (*non* Sternb.), Végétaux fossiles des terrains houillers de la Belgique, pl. 31. fig. 344.

#### *Remarks on synonymy of* N. TENUIFOLIA *Schloth.* (*sp.*).

N. GIGANTEA.

Brongniart (**5**, p. 241) and Schimper (**18**, vol. i. p. 438) noted the resemblance of *N. tenuifolia* Schloth. (sp.) to *N. gigantea* Sternb., the latter stating that *N. tenuifolia* Schloth. (sp.) is distinguished by its smaller pinnules, which are closer together, and by the distinctly heart-shaped base; also the pinnules are less caducous.

N. HETEROPHYLLA.

Zeiller (**20**, p. 275) states that *N. tenuifolia* Schloth. (sp.) greatly resembles *N. heterophylla* Brongn. in many respects, and that many authors have suggested uniting them, seeing in them very near varieties or even forms of one and the same species. Zeiller (**20**, p. 275) was unable to reconcile himself to this point of view, and gave his reasons why they should not be united. Zeiller's view that these two species should not be united is in my opinion the correct one, and for the same reasons, namely that *N. tenuifolia* Schloth. (sp.) appears to offer in the form of its pinnules and in its nervation perfectly constant characters without transition towards *N. heterophylla* Brongn.

Certain forms of *Neuropteris* pinnæ which have a close relationship to *N. tenuifolia* Schloth. (sp.) are included in *N. heterophylla* Brongn.

Zeiller (**20**, p. 274) gives the impression that he considered all specimens of *N. tenuifolia* Schloth. (sp.) to be of the same size, and that he did not recognize the possibility of smaller and less mature forms. These younger forms have been, I believe, frequently grouped with *N. heterophylla* Brongn.

N. FLEXUOSA.

The same author also notes a slight resemblance between *N. tenuifolia* Schloth. (sp.) and *N. flexuosa* Sternb., but thinks they can be easily distinguished. My investigations, both on the published figures of other authors and upon material, seen in collections and in the field, have shown the existence of a series of intermediate forms linking up *N. tenuifolia* Schloth. (sp.), *N. flexuosa* Sternb., and *N. gigantea* Brongn.

In the specimen (now in the possession of the Bristol Museum) figured on Pl. **5**. it will be clearly seen that while the uppermost pinnules undoubtedly belong to *N. tenuifolia* Schloth. (sp.), the lower ones have the characters associated with *N. flexuosa* Sternb. In fact, given one of these lateral pinnæ separately, it would certainly be identified as *N. flexuosa* Sternb.

### *Diagnosis of* N. TENUIFOLIA *Schloth. (sp.).*

Although Schlotheim is the author of the species, he does not give a diagnosis, evidently considering his figure to be sufficient. Brongniart's diagnosis (**5**, p. 241), which is as follows, agrees with Schlotheim's figure.

*N.* foliis bipinnatis, pinnis elongatis; pinnulis approximatis contiguis vel subimbricatis, oblongis, apice attenuatis obtusi, basi cordatis, nervo medio valde notato, apice evanescente; nervulis obliquis, arcuatis, dichotomis, approximatis, tenuissimis; pinnulâ terminali lanceolata acuminata, basi cuneata sublobata, lateralibus triplo longiore.

*Distribution.*

This species occurs in the Upper, Transition, and Middle Coal Measures, but has not, so far as I am aware, been recorded from the Lower Coal Measures. Its maximum is reached in the Upper Coal-Measure Series. It is found in all the British coalfields.

### NEUROPTERIS MACROPHYLLA Brongn.

1822. *Neuropteris macrophylla* Brongniart, Histoire des Végétaux fossiles, p. 235, pl. 65. fig. 1.
1869. —— —— Schimper, Traité de Paléontologie Végétale, vol. i. p. 434.
1881. —— —— Renault, Cours de Botanique Fossile, p. 173.
1888. —— —— Kidston, Proc. Roy. Soc. Edin. vol. xxxiii. pt. ii. (1888), p. 354, pl. 21. fig. 2 & pl. 22.
1843. *Neuropteris Clarksoni* Lesquereux, in Roger's Geology of Pennsylvania, vol. ii. p. 857, pl. 6. figs. 1–4.
1879. —— —— Lesquereux, Coal Flora of Pennsylvania, p. 94, pl. 9. figs. 1–6.
1886. *Neuropteris Scheuchzeri* Kidston (*non* Hoffmann), Catalogue Palæozoic Plants, p. 95.

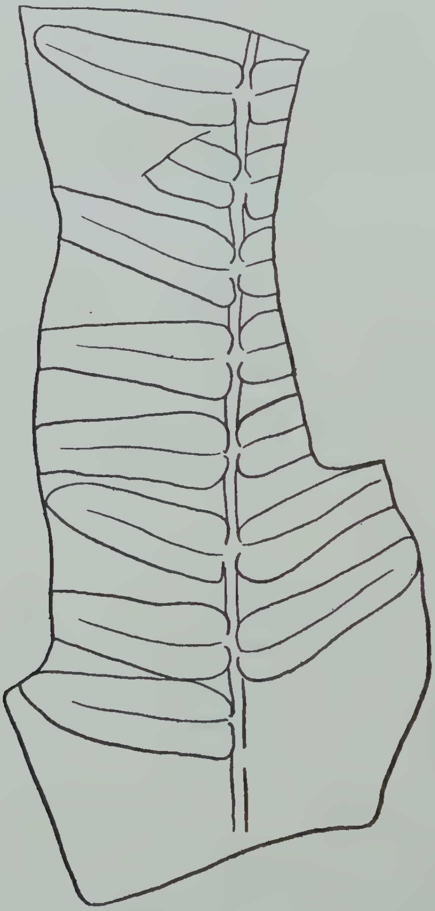
### *Remarks on synonymy of* N. MACROPHYLLA *Brongn.*

Most of the older authors in commenting on this species remark on its close resemblance to the recent fern *Osmunda*, but they differ as to which species of the latter it most resembles. Brongniart compares it to *O. regalis* Linn., whilst Renault and Schimper consider it more closely related to *O. spectabilis* Willd.

NEUROPTERIS SCHEUCHZERI.

The pinnules of *N. macrophylla* Brongn. are very caducous (which suggests that they are fully mature), and when found isolated they are difficult at first sight to distinguish from those of *N. Scheuchzeri* Hoffm. A careful examination of the pinnules of the latter species reveals the presence of hairs on the upper surface of the pinnule, a feature shared, so far as is known at present, with no other species of *Neuropteris*.

FIG. 4 *a*.



*Neuropteris macrophylla* Brongn. after Brongniart (reduced).

N. TENUIFOLIA.

At Crawcrook Clay Pit, Co. Durham, I have seen numerous specimens intermediate in character between the smaller forms of *N. macrophylla* Brongn. and the larger forms of *N. tenuifolia* Schloth. (sp.). These link up *N. macrophylla* Brongn. with the four species previously described (*N. flexuosa* Sternb., *N. gigantea* Sternb., *N. ovata* Hoffm., and *N. tenuifolia* Schloth., sp.).

NEUROPTERIS AURICULATA.

Certain forms of *N. macrophylla* Brongn. are not unlike *N. auriculata* Brongn., and there is good reason to believe that they are intermediate forms connecting the two species.

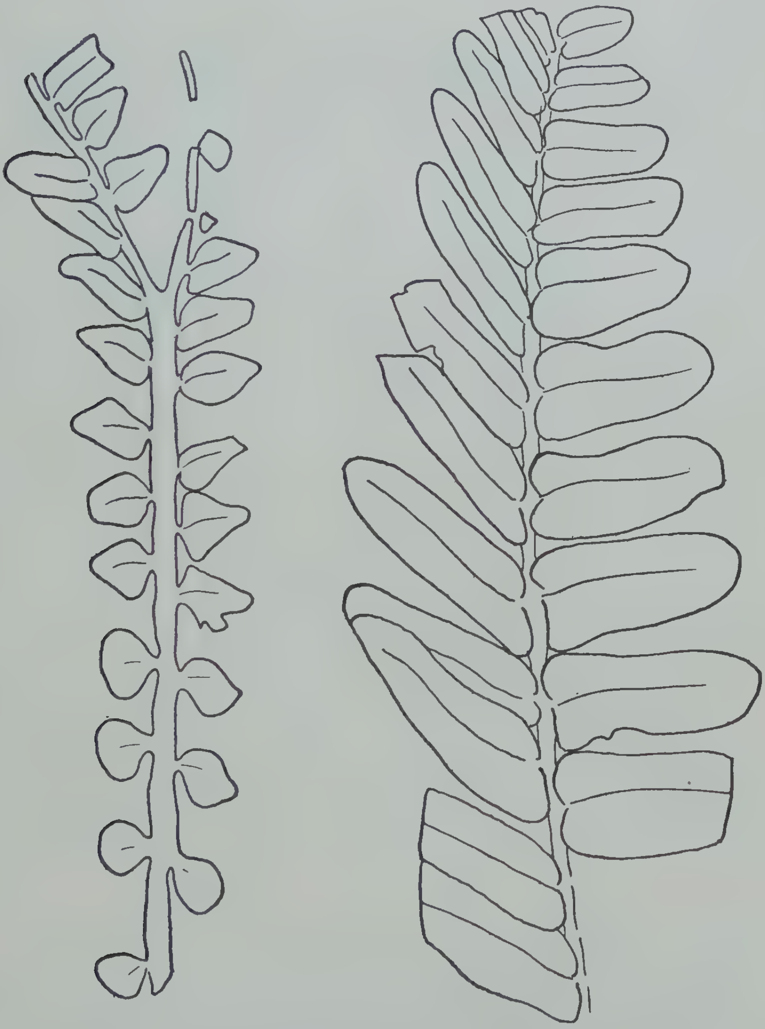


FIG. 4 *b*.

FIG. 4 *c*.

*Neuropteris macrophylla* Brongn., both after Kidston (reduced).

### *Diagnosis of* N. MACROPHYLLA *Brongn.*

*N.* foliis pinnatis vel bipinnatis, pinnulis distantibus oblongis, obtusis, basi dilatibus cordatis, angulo inferiore paulatim extenso ; nervo medio valde notato ; nervulis dichotomis, e nervo medio nascentibus, arcuatis.

The frond was very large, with the pinnæ dividing by a series of bifurcations. The pinnules, which alternate on the rachis, are of varying size and shape, being triangular, lanceolate-acute, oblong-obtuse, and cyclopteroid. As in most species of *Neuropteris*, the midrib is distinct in the greater part of the pinnule, but breaks up by a series of dichotomies into numerous fine veins, which are arched and usually forked four times.

### *Distribution.*

This species occurs in the Upper, Transition, and Middle Coal Measures, but has not yet been recorded from the Lower Series. The maximum development occurs in the Upper Coal Measures, where it is particularly common. It is recorded from five of the seven coalfields of England.

## NEUROPTERIS HETEROPHYLLA Brongn.

1822. *Filicites* (*Neuropteris*) *heterophyllus* Brongniart, Classification des Végétaux fossiles, pp. 33, 89, pl. 11. figs. 6 *a*, 6 *b*.
1828. *Neuropteris heterophylla* Brongniart, Prodrôme, p. 53. Id., Histoire des Végétaux fossiles, p. 243, pl. 71; pl. 72. fig. 2.
1833. *Neuropteris Brongniartii* Sternberg, Essai d'un Exposé geognostico-botanique de la flore du monde primitif, vol. ii. fasc. V., VI. p. 72.
1830. *Neuropteris Loshii* Brongniart, Histoire des Végétaux fossiles, p. 242, pl. 72. fig. 1; pl. 73.
1836. *Gleichenites neuropteroides* Goeppert, Systema filicum fossilium, p. 186, pls. 4–5.
1838. *Filicites Goepperti* Presl, in Sternberg, Essai d'un Exposé geognostico-botanique de la flore du monde primitif, vol. ii. fasc. VII.–VIII. p. 175.
1862. *Odontopteris oblongifolia* Roemer, Palæontographica, vol. ix. p. 31, pl. 7. fig. 1.
1868. *Odontopteris britanica* Roehl, Palæontographica, vol. xviii. p. 41 (pars), pl. 20. fig. 4.
1868. *Odontopteris obtusiloba* Roehl, Palæontographica, vol. xviii. p. 42, pl. 16. figs. 12–15.

### *Remarks on synonymy of* N. HETEROPHYLLA *Brongn.*

After examining a large number of specimens identified by many various workers as *N. heterophylla* Brongn., I am doubtful whether this can be considered as a valid species, or whether many specimens identified under this specific name will not, in most cases, prove to be young or varietal forms of other well-known species.

### N. LOSHII.

As I have previously stated in dealing with *N. flexuosa* Sternb., I have become convinced, after careful study of much material, that the form known as *N. Loshii* Brongn. and included by most authors as a synonym of *N. heterophylla* Brongn. is really an immature condition of *N. flexuosa* Sternb.

Again, a few of the forms included in *N. heterophylla* Brongn. are dimorphic, a character which is not confined to this species. Arber (**1**, p. 171) has shown that the species *N. obliqua* Brongn. is also dimorphic, having large major pinnules and smaller bipinnate minor pinnules, and that both frequently occurred on the same pinnæ.

NEUROPTERIS FLEXUOSA.

In the specimen figured by Brongniart (5, pl. 71) many of the lateral pinnæ show the characters usually associated with *N. flexuosa* Sternb. Brongniart's example is clear evidence of the existence of intermediate forms linking the two species *N. heterophylla* Brongn. and *N. flexuosa* Sternb.

N. TENUIFOLIA.

Schimper (18, vol. i. p. 438) in referring to *N. heterophylla* Brongn. says, "This species does not appear to be distinct from *N. tenuifolia* Schloth." Brongniart had already expressed doubts when he said, "It is possible, however, that these two plants are only varieties of the same species." "I feel tempted," he goes on to say, "to go even further and unite with it *N. Loshii* Brongn., *N. tenuifolia* Schloth., and *N. Soretii* Brongn., as I possess specimens of these different plants which appear to offer passages between each other." I have found similar intermediates.

The specimen figured by Zeiller (20, pl. 43) under the designation *N. heterophylla* Brongn. is evidently the apical portion of a large frond belonging to the species-group *N. flexuosa* and probably to the type-species *N. flexuosa* Sternb. itself (see text-fig. 1, p. 298). Two forms of pinnules occur on the frond. Those about the middle of the specimen are very similar in character to those of *N. tenuifolia* Schloth., but where the pinnæ become compound they take on the form and character we associate with *N. flexuosa* Sternb.

The portion of frond figured on pl. 44 (Zeiller, 20, pl. 44) apparently grew lower down on the rachis. In one part of it the dimorphic character is clearly shown, for one side of the rachis bears single pinnules of the form known as *N. tenuifolia* Schloth., whilst the other has pinnules similar to those of *N. flexuosa* Sternb.

The diverse characters of the many specimens included in the species *N. heterophylla* Brongn. and the laxity allowed by the original diagnosis has caused the species to become a dumping ground for all doubtful species of pinnæ.

### *Diagnosis of* N. HETEROPHYLLA *Brongn.*

*N.* foliis maximis tripinnatis, quandoque e basi bifurcatis, pinnis alternis magis minusve elongatis, superioribus brevissimis; pinnulis formâ diversissimis, pinnarum inferiorum oblongis subovatis; intermediarum ovatis, superiorum subrotundis minimis paucioribus; terminalibus oblongo-lanceolatis, basi cuneatis, lateralibus multo longioribus; omnibus basi cordatis, nervulis arcuatis tenuissimis.

*Distribution.*

Throughout the Coal-Measure Series and in all the coalfields of Great Britain.

### NEUROPTERIS RARINERVIS Bunbury.

1847. *Neuropteris rarinervis* Bunbury, Quart. Journ. Geol. Soc. vol. iii. pp. 425, 438, pl. 22.
1870. *Neuropteris coriacea* Lesquereux, Geol. Surv. of Illinois, vol. iv. p. 387, pl. 8. figs. 7–8. Id., Coal Flora, p. 111, pl. 18. fig. 6.
1876. *Neuropteris attenuata* Boulay (*non* Lindley & Hutton), Terr. houill. du Nord de la France, pp. 30, 74, pl. 4. fig. 1.
1878. *Neuropteris heterophylla* Zeiller (*non* Brongniart), Expl. carte géol. France, vol. iv. pl. 164. fig. 2, p. 49 (part).

#### *Remarks on synonymy of* N. RARINERVIS *Bunbury.*

It is with doubt that I include this species in the species-group *N. flexuosa.* I have been unable to find any species of *Neuropteris* with which *N. rarinervis* Bunbury, appears to have any true affinity, unless it be with *N. flexuosa* Sternb., which it resembles in the form of its pinnæ and pinnules. *N. rarinervis* Bunbury, remains for the time being an isolated species, having no known affinities with any of the present species-groups.

N. FLEXUOSA.

In general form of the frond and in the outline of the pinnules it much resembles *N. flexuosa* Sternb., and upon a hasty examination it might be mistaken for that species, from which it differs in its venation. The veins of *N. rarinervis* Bunbury, are farther apart than in any other member of the genus, and though arched in the manner characteristic of the genus, are scarcely ever more than twice forked, indeed in many of the smaller pinnules only once. The comparatively few thick veins ought to render it an easy species to distinguish. It is also the only species of *Neuropteris* in which I have found the number of veins per centimetre to be reliable as a diagnostic character.

#### *Diagnosis of* N. RARINERVIS *Bunbury.*

The frond is bipinnate, the main stalk striated and rather slender in proportion; the pinnæ partly opposite and partly alternate, narrow and almost linear in their general outline. Pinnules closely set, but not usually overlapping, oblong, rounded at the end, slightly waved at the edges, oblique and somewhat dilated at the base, where they are more or less auricled; they are convex, and appear to have been of a firm consistence; their surface is smooth and shining. In length they vary from $\frac{1}{5}$ to $\frac{1}{2}$ inch, those of the lower pinnæ being in general the largest and most elongated. The veins are strong and prominent. Towards the top of the frond the pinnules run into one another, so that the pinnæ become merely sinuated and a few of the uppermost are completely undivided.

*Distribution.*

This species is found in the Upper, Transition, and Middle Coal-Measure Series and in most of the coalfields, but it is never common.

NEUROPTERIS SCHEUCHZERI Hoffm.

1826. *Neuropteris Scheuchzeri* Hoffmann, in Keferstein's Teutschland geognotisch-geologisch dargestellt, vol. iv. p. 156, pl. 1 *b*. figs. 1–4.

1830. *Neuropteris angustifolia* Brongniart, Histoire des Végétaux fossiles, p. 231, pl. 64. figs. 3–4.

1830. *Neuropteris acutifolia* Brongniart, Histoire des Végétaux fossiles, p. 231, pl. 64. figs. 6–7.

1832. *Neuropteris cordata* Lindley & Hutton (*non* Brongn.), Fossil Flora, vol. i. pl. 41.

1858. *Neuropteris hirsuta* Lesquereux, in Rogers, Geol. Pennsyl. vol. ii. p. 857, pl. 3. fig. 6; pl. 4. figs. 1–16.

1862. *Dictyopteris Scheuchzeri* Roemer, Palæontographica, vol. ix. p. 30, pl. 9. fig. 1.

1886. *Neuropteris Scheuchzeri* Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 251, pl. 41. figs. 1–3.

1902. —— —— Kidston, Végétaux Houillers dans le Hainaut Belge, p. 80.

### *Remarks on synonymy of* N. SCHEUCHZERI *Hoffm.*

It is with some doubt that I suggest the placing of *N. Scheuchzeri* Hoffm. in the species-group *N. flexuosa.* At first sight the pinnules of this species, especially when found isolated (which is often the case), seem to be a large form of *N. tenuifolia* Schloth. or *N. macrophylla* Brongn. Careful examination will reveal, however, the presence of fine hairs, which occasionally give the appearance of anastomosing veins covering the surface of the pinnule. This is the only known species of *Neuropteris* which is hairy. The frequent presence of a small basal pinnule on the lower side of the large pinnule is another distinguishing feature.

All the specimens of *N. Scheuchzeri* Hoffm. that I have seen have had the appearance of being fully mature. The presence of hairs may be a condition of maturity, and the young fronds, being destitute of such hairs, are yet unrecognized. In all probability they must be looked for amongst the many examples referred to the species-group *N. flexuosa.* Conversely, it may be that *N. Scheuchzeri* Hoffm. is not hairless in its immature stages, but that the hairs, being very fine and delicate, were lost during fossilisation. This, I think, is the more likely.

### *Diagnosis of* N. SCHEUCHZERI *Hoffm.*

Frond very large, tripinnate. Secondary rachis 10–20 mm. wide, marked, like the rachis of the third order, with fine regular longitudinal striæ, and having, on the rachis between the secondary pinnæ, pinnules like those on the pinnæ. Secondary pinnæ alternate or sub-opposite, 6–16 cm. apart, encroaching a little on each other, 6–15 cm. wide, 20–60 cm. long, linear-lanceolate or oval-lanceolate in shape, sometimes slightly restricted at the base, having the same width over nearly the whole of their extent and then tapering to a point. Pinnules alternate or sub-opposite, nearly sessile, easily caducous, straight or curved back like a scythe, 2–10 cm. long, 8–25 mm. wide, touching a little along their margins or else clearly separated, tapering to a sharp point at the apex, rounded at the base of the lower side or often enlarged into a slightly projecting ear-shaped structure, truncated very obliquely on the upper side and flanked by a small orbicular or oval pinnule rounded at the top, 5–12 mm. wide and 2–8 mm. long. Towards the top of the secondary pinnæ this small basal pinnule is united to the large pinnule, of which the base is then cordiform.

Terminal pinnule of the secondary pinnæ is a little longer than the preceding ones, but equally pointed at the apex. The pinnules attached directly on the secondary rachis are generally a little shorter than the others, always have two small independent pinnules at the base, one above and one below, both rounded or obtusely pointed at the apex, and being nearly 15 mm. long, sometimes only the upper small pinnule remains independent, as on the secondary pinnæ, and the other completely united, simply forms a lobe at the base of the large pinnule.

Median vein clear, dividing a little beyond the middle of the pinnule; secondary veins arise at a very sharp angle, then gradually arched, dichotomising several times into fine compact veinlets. Lower surface of the pinnule, large or small, bristling with stiff, scattered hairs, 1·5–2 mm. or nearly 3 mm. long, lying almost parallel to the median vein. (Zeiller, **21**, p. 252.)

*Distribution.*

*N. Scheuchzeri* Hoffm. is found in the Upper, Transition, and Middle Coal Measures, being particularly common in the Upper Coal Measures.

### *Conclusions drawn from a critical study of the Species-group* N. FLEXUOSA.

A close study, extending over four years, on some hundreds of *Neuropteris* pinnæ, has led me to the conclusion that the five species, *N. flexuosa* Sternb., *N. ovata* Hoffm., *N. gigantea* Sternb., *N. tenuifolia* Schloth. (sp.), and *N. macrophylla* Brongn., are closely linked to each other by a series of intermediates, and that they are more sharply defined from all other species. The shape of the pinnæ, and the size, form, and venation of the pinnules of specimens identified as belonging to one or other of these five species undoubtedly show that there is some connection between these species.

The general outline of the pinnæ shows a great similarity throughout the five species. The largest pinnules are found at the base of the pinnæ, and their size gradually diminishes as they are traced towards the apex, which may or may not end in a terminal pinnule. This terminal pinnule is usually larger and of a slightly different shape from the lateral pinnules, having its greatest width at the base rather than nearer the middle, as in the lateral pinnæ. The lateral pinnæ are, with one exception—*N. rotundifolia* Brongn.—longer than they are broad. The pinnules of *N. tenuifolia* Schloth. are about the only ones which afford comparatively little difficulty to identify when found isolated, while those of *N. gigantea* Sternb. and *N. flexuosa* Sternb.

are frequently extremely difficult to separate. In all the species the venation is similar, both in the relative thickness and in the spacing of the veins, and for this reason the number of veins per centimetre can possess no diagnostic value.

*N. flexuosa* Sternb. is the species around which the other four species may be grouped. Typically the species is characterized by a much enlarged terminal pinnule roughly triangular in outline, while the lateral pinnules are longer than they are broad, being in the ratio of 2 : 1. The veins in all the pinnules are moderately fine and fairly close together, the number of veins per centimetre of margin varying between 25–60 according to the age of the pinnule, and the position of the marked centimetre on the margin, whether near the apex or base of the pinnule. The usual number of veins to be found coming to the margin in the middle of a mature leaf is about 35, but it is not a number to be relied on for identification purposes. The veins usually fork twice after leaving their point of origin. In no case does the mid-rib extend to the apex of the pinnule, but generally breaks up by a series of bifurcations. Between the typical form and the species *N. gigantea* Sternb. occur numerous intermediate forms, which by their varying characters connect *N. flexuosa* Sternb. and *N. gigantea* Sternb. together. In the absence of the enlarged terminal pinnule of *N. flexuosa* Sternb. it is frequently difficult to distinguish this species from *N. gigantea* Sternb., as the characters of the lateral pinnæ are so alike.

*N. ovata* Hoffm. can hardly be regarded as an intermediate species, but rather as an immature condition of *N. flexuosa* Sternb.

Specimens of *N. flexuosa* Sternb. are frequently found in which the terminal pinnule, whilst retaining its characteristic shape, does not become much larger than the lateral pinnules, and where the rounded apex gradually becomes more acute. These examples are intermediates between *N. flexuosa* Sternb. and *N. tenuifolia* Schloth. Where several pinnæ are found in organic connection, it will frequently be seen that some pinnules retain more of the characters of *N. flexuosa* Sternb. than do the remainder.

*N. gigantea* Sternb. has some relation to *N. flexuosa* Sternb. and *N. tenuifolia* Schloth. Although the greatest number of specimens of this species found agree with the type, others frequently occur having affinities either with *N. flexuosa* Sternb. or *N. tenuifolia* Schloth. (sp ).

Large pinnules of *N. tenuifolia* Schloth. often bear a close resemblance to the smaller pinnules of *N. macrophylla* Brongn., and these form the intermediates between the two species. Certain of the specimens now identified as *N. macrophylla* Brongn. can be designated as connecting-links between this group of species now under consideration, which I propose calling the species-group *N. flexuosa*, and the two other species-groups with which I shall deal later.

From materials I have collected, I have been able to select a series of specimens which exhibit the relationship existing between all the species in the species-group *N. flexuosa* (see Pl. **6**). The series includes specimens which are typical of the following species:—*N. flexuosa* Sternb., *N. gigantea* Sternb., *N. tenuifolia* Schloth. (sp.), and *N. macrophylla* Brongn., and also a number of intermediate forms linking the species to each other. The relationships are so well established by these examples that it would seem justifiable to conclude that the four species have been founded upon portions of fronds taken from different parts of the same plant. I am of the opinion that the differences which are found to occur in these apparent "species" are only such as can be accounted for by the position occupied on the plant or rachis or by a difference in age.

A frond belonging to the species-group *N. flexuosa* may, I think, have either *N. tenuifolia* Schloth. at its apex, and on its becoming pinnate, break up into pinnæ having the characters of *N. flexuosa* Sternb., or, on the other hand, the apical portion may be of the *N. flexuosa* Sternb. type, while the lower pinnules may have the characters of *N. tenuifolia* Schloth. Probably the first type belonged to pinnæ of the primary order and possibly the secondary as well, if the frond were tripinnate, while the other pinnæ were of the second type.

The reason for such a detailed study of this species-group is that most of its members are common throughout the coalfields of Britain, and therefore a far greater amount of material has been available for examination.

### *Characters of Species-group* N. FLEXUOSA.

The pinnæ have the larger pinnules at the base of the rachis, while the remaining pinnules gradually decrease in size as they approach the apex, which is usually terminated by the largest pinnule. This apical pinnule, when present, is of a characteristic shape, being roughly triangular. This type of apical pinnule is found only on specimens belonging to this species-group. The lateral pinnæ are either very shortly stalked or else attached by a small portion of the base; in shape they are longer than broad, with the apex varying from round to acute. The veins are moderately fine and fairly close together, arising from a mid-rib which extends about two-thirds of the way up the lamina; they usually fork twice after leaving their point of origin.

## 4 B. **Species-group** N. OBLIQUA.

Synonymy of *N. obliqua* Brongn. See Arber, Journ. Linn. Soc., Bot. vol. xlvi. (1922) p. 207.

### *Remarks on synonymy of* N. OBLIQUA *Brongn.*

The late Dr. E. A. Newell Arber gave so able and concise a statement of the relationships existing between *N. obliqua* Brongn., *N. callosa* Lesq., and *N. impar* Weiss (**1**, p. 201) that nothing more need be added. He recognized the dimorphic character of *Neuropteris* fronds, and after careful research came to the conclusion that *N. acuminata* Schloth. sp. and *N. impar* Weiss were both major pinnules belonging to *N. obliqua* Brongn. As he pointed out, examples of what is probably a closely-allied species, namely *N. callosa* Lesq., have frequently been wrongly identified as *N. obliqua* Brongn. These two species, like those in the previously-mentioned species-group, appear to be connected by a series of intermediates.

Unfortunately the members of this species-group are comparatively rare, a fact which renders it difficult to obtain good material.

The specimen illustrated on pl. 183 of Lindley & Hutton's 'Fossil Flora,' and identified by them as *N. heterophylla*, is a specimen of *N. obliqua* Brongn., showing both major and minor pinnules. This is another instance of the totally different types which have been grouped together as *N. heterophylla* Brongn.

### *Diagnosis of* N. OBLIQUA *Brongn.*

The following description is that given by Arber (**1**, p. 211):—"Frond dimorphic, composed entirely of minor or of major pinnules, or containing pinnules of both types. Minor pinnules small, up to 2 cm. long and nearly 1 cm. broad, often considerably smaller, elongately oval or elongately triangular, more or less parallel-sided, attached to the axis by the whole base or, in the broader types, only by a part of the base. Apical pinnule very large or long and narrow. Lateral nerves very little arched, sinuous, each dichotomising 2–3 times, markedly distant from one another in centre of leaf. Major pinnules very variable in size and shape, even in the same pinna, lanceolate (up to $2{\cdot}5 \times 1$ cm.), ovate lanceolate (up to $5 \times 2{\cdot}5$ cm.), oval or semicyclopteroid (about $3{\cdot}5 \times 2{\cdot}5$ cm.), sometimes very broad and unsymmetrical, attached to the rachis by a very small part of the base, which, however, is sometimes sufficiently broad to allow of the origin of some of the basal veins directly from the rachis. The lanceolate pinnules are frequently lobed or divided into minor pinnules at the base. The cyclopteroid-like pinnules have a broader point of attachment and a more radiating nervation, partly arising directly from the rachis. The lateral nerves are more frequently dichotomised than in the minor pinnules, but possess a similar inclination and are also sinuous in their course."

### *Distribution.*

This species is found in the Middle and Lower Coal Measures, but is nowhere very common.

### NEUROPTERIS CALLOSA Lesq.

1879–80. *Neuropteris callosa* Lesquereux, Geol. Survey Pennsylvania, p. 115, pl. 16. figs. 1–4 (? figs. 5–8).

1909. *Neuropteris obliqua* Arber, in Quart. Journ. Geol. Soc. vol. lxv. p. 26, pl. 1. fig. 3.

1911. —— —— Kidston & Jongmans, Arch. Néerl. Sci. Exact. et Nat. ser. 3 B vol. i. p. 25, pl. (unnumbered), fig. 3.

### *Remarks on synonymy of* N. CALLOSA *Lesq.*

Although I quite agree with Dr. Arber in his statement that *N. obliqua* Brongn. and *N. callosa* Lesq. are distinct species, I think that some specimens now otherwise difficult to identify will prove to be intermediates between the two species.

Arber (**1**, p. 215) suggests a possible relationship between *N. callosa* Lesq., *N. tenuifolia* Schloth., and *N. heterophylla* Brongn. If this suggestion is correct, and from my researches I think it is, then the two species-groups of *N. flexuosa* and *N. obliqua* will be connected with each other by intermediates in the same manner as are the individual species within these species-groups.

### *Diagnosis of* NEUROPTERIS CALLOSA *Lesq.*

Frond large, tri- or ? quadripinnate. Penultimate pinnæ broad, often, but not always, with broad axis; ultimate pinnæ lanceolate, axis very slender. Pinnules typically Neuropteroid, inserted by a very small part of the base, oval or elongately oval, varying much in size from 4 mm. up to 20 mm. or more in length, entire, broadly rounded at the apex, markedly cordate, almost eared, at the base, closely set on the axis, and frequently overlapping one another. Pinnules markedly caducous. Nervation clearly marked, but nerves fine, all nearly equally strong and equally placed. Lateral nerves all arising from the median nerve, not crowded, somewhat arched, flexuous in their course, dichotomising one to three times. Lamina between veins frequently punctate. Terminal pinnule rather small, elongately lanceolate. (Arber, *op. cit.* i. p. 214.)

*Distribution.*

*N. callosa* Lesq. is found in several of the British coalfields on the horizon of the Transition and Middle Coal Measures

### NEUROPTERIS SCHLEHANI Stur.

1868. *Neuropteris tenuifolia* Roehl (*non* Sternb.), Palæontographica, vol. xviii. p. 36, pl. 20. fig. 5.
1877. *Neuropteris Schlehani* Stur, Culm Flora, ii, p. 289, pl. 28. figs. 7, 8. Weiss, Aus d. Steink. p. 15, pl. 15. fig. 92.
1877. *Neuropteris Dluhoschi* Stur, Culm Flora, ii. p. 289, pl. 28. fig. 9.
1879. *Neuropteris Elrodi* Lesquereux, Atlas to the Coal Flora, p. 3, pl. 13. fig. 4. Lesquereux, Coal Flora, p. 107; iii. p. 735, pl. 96. figs. 1–2.
1881. *Neuropteris gigantea* Achepohl (*non* Sternb.), Niederrh.-Westfäl. Steinkohl. p. 56, pl. 16. fig. 2.
1886. *Neuropteris Schlehani* Zeiller, Flore fossile du Bassin houiller de Valenciennes, p. 280.

### *Remarks on synonymy of* N. SCHLEHANI *Stur.*

N. TENUIFOLIA and N. OBLIQUA.

The general character of the venation and the shape of the pinnules of the apical portion of the primary pinnæ bears a close resemblance to certain forms of *N. tenuifolia* Schloth. At the same time, the characters of the pinnules on the secondary pinnæ suggest affinities with members of the species-group *N. obliqua,* particularly with the minor pinnules of *N. obliqua* Brongn. Thus it would appear that the species under consideration might be a connecting-link between these two species-groups.

### *Diagnosis of* N. SCHLEHANI *Stur.*

Fronds of great size, at least tripinnate. Secondary rachis 3–5 mm. wide, marked by fine irregular striations. Primary pinnæ straight, being at least 40 cm. long, with a width of 12–20 cm., lanceolate in shape, remaining the same size for two-thirds or three-quarters of their length, then rapidly contracting to a pointed apex, bipinnate for their greatest part, simply pinnate at their extremity. Uppermost primary pinnæ probably simply pinnate.

Secondary pinnæ of the primary pinnæ alternate or sub-opposite, straight or flexuous, 12–25 mm. apart, usually overlapping a little, 4–13 cm. long, 8–30 mm. wide, linear-lanceolate or narrowly oval-lanceolate in shape; margins nearly parallel, sometimes slightly contracted at the base, tapering to a point at the apex, simply pinnate or replaced towards the apex of the primary pinnæ by large simple pinnules; margin lobed or undulating at the base, or else entire, linear, tapering to an obtusely-pointed apex 1–4 cm. long, 2–6 mm. wide.

Pinnules alternate or sub-opposite, narrow or slightly arched, rounded at the margins, contiguous or slightly separated from each other; form and size very variable according to the position they occupy, 3–20 mm. long, 2–6 mm. wide, sessile or with short stalks, attached by a single point except at the ends of the pinnæ, where they are decurrent on the rachis, heart-shaped at the base, oval or more generally linear in shape, contracted towards the apex to an obtuse or obtusely-pointed apex. Terminal pinnule of secondary pinnæ longer than those preceding it, linear, contracted towards the apex to an obtuse or obtusely-pointed apex.

Median vein clear, marked on the upper side by a very accentuated furrow, which goes almost to the top of the pinnule; lateral veins numerous, very strong and slightly raised, arising at a short angle, very rapidly arching, dichotomising 2–3 times into fine veins, which reach the margins almost at right angles. (Zeiller, **20**, p. 280.)

*Distribution.*

*N. Schlehani* is found in the Transition and Middle Coal-Measure Series, and is recorded from these horizons in the Radstock and South Wales Coalfields. I do not know of the species being recorded from any other horizon or locality.

### NEUROPTERIS RECTINERVIS Kidston.

1887. *Neuropteris rectinervis* Kidston, in Trans. Roy. Soc. Edin. vol. xxxv. (1887) pt. v. p. 314.

### *Remarks on* N. RECTINERVIS *Kidston.*

N. SCHLEHANI.

In both this species and *N. Schlehani* Stur the venation is characterized by the very wide angle most of the lateral veins make with the margin of the pinnule. In *N. rectinervis* Kidston the angle is usually slightly wider than in *N. Schlehani* Stur, being almost a right angle (in this character the venation resembles that found in the genus *Alethopteris*). In both *N. rectinervis* Kidston and *N. Schlehani* Stur the mid-rib is very distinct, and extends almost to the apex of the pinnule, while the lateral pinnules are oval or oblong. In *N. Schlehani* Stur the terminal pinnule is usually longer than that found in *N. rectinervis* Kidston. My observations have led me to conclude that there is a fairly close relationship between the two species. I am aware of the fact that *N. rectinervis* Kidston is regarded as a Lower Coal-Measure form, while *N. Schlehani* Stur is recorded from the Middle and Transition Series. This fact does not however, I think, prevent a relationship existing between them, but rather suggests that the newer form may have evolved from the older form of the Lower Coal Measures.

### *Diagnosis of* N. RECTINERVIS *Kidston.*

Pinnules sessile, alternate oval or oblong, blunt, approximate or slightly separated; margin entire and free from plications. Mid-rib very distinct and extending almost to the apex. Lateral veins numerous, distinct, fine, springing from the mid-rib with a gentle curve and then running the greater part of their course almost at right angles to the margin of the pinnule, usually once, but occasionally twice, divided. Terminal lobe long.

*Distribution.*

Middle Coal Measures of Radstock, and Northumberland and Durham.

### *Conclusions drawn from a critical study of the Species-group* N. OBLIQUA.

I include *N. Schlehani* Stur and *N. rectinervis* Kidston in the species-group *N. obliqua*, but with some doubt. In many characters, chiefly the shape and general outline of the pinnules, *N. Schlehani* Stur resembles some of the minor pinnules of *N. obliqua* Brongn., but at the same time the venation and outline of some of the pinnules also suggest affinities with *N. tenuifolia* Schloth., a species included in the species-group *N. flexuosa*. It would almost seem, therefore, that in the species *N. Schlehani* Stur we have a form which is an intermediate or connecting-link between the two species-groups. These remarks also apply to the species *N. rectinervis* Kidston.

A characteristic feature of the pinnæ placed in this species-group is the tendency of the apical pinnule to become decurrent on the rachis, while many of the lateral pinnules are attached by a portion of their base, through which veins having their origin in the rachis, pass into the pinnule. This character of the lateral veins is one shared by members of the next species-group. There is, in fact, a close relationship existing between the members of the species-group *N. obliqua* and those of the species-group *N. auriculata*. In shape, size, and venation some of the major pinnules of *N. obliqua* Brongn. are very similar to those identified as *N. auriculata* Brongn., and it is these pinnules which form the chief connecting-link.

### *Characters of Species-group* N. OBLIQUA.

The pinnæ are characterized by comparatively long and narrow terminal pinnules, which have a tendency to become decurrent on the rachis. The lateral pinnules of the "major-pinnule" type are large and not unlike some of those found on specimens belonging to the species-group *N. flexuosa*. Those of the "minor-pinnule" type are small and have a rounded apex. Both kinds of pinnules may be attached either by short foot-stalks or else by a portion of the base; in the latter case some of the veins have their origin in the rachis. The mid-rib is clearly marked and extends almost to the apex of the pinnule. Like the apical pinnule, the lateral pinnules show a tendency to become decurrent. The lateral veins are numerous and fork two or three times.

## 4 C. **Species-group** N. AURICULATA.

### NEUROPTERIS AURICULATA Brongn.

1828. *Neuropteris auriculata* Brongniart, Histoire des Végétaux fossiles, p. 236, pl. 66.
1869. —— —— Schimper, Traité de Paléontologie Végétale, vol. i. p. 443.
1880. —— —— Zeiller, Végétaux fossiles du terrain houiller de la France, p. 52.

### *Remarks on synonymy of* N. AURICULATA *Brongn.*

This large-leafed form of *Neuropteris* pinnule is easily distinguished from any of the species forming the two other species-groups. The almost completely sessile pinnules, in which a definite median vein appears to be absent, are quite unlike any other species, except perhaps certain large forms of *N. macrophylla* Brongn., which appear to be connecting-links between the two species-gronps.

### *Diagnosis of* N. AURICULATA *Brongn.*

Fronds large, bipinnate, pinnæ alternate, rachis broad, with cyclopteroid pinnules. Pinnules large (up to 4·5 × 2·5 cm.), sessile, frequently attached by a broad portion of the base, through which the veins pass from their point of origin on the rachis. Apex broadly acute or rounded, margins more or less parallel. Veins fine and compact, median vein almost or entirely absent.

*Distribution.*

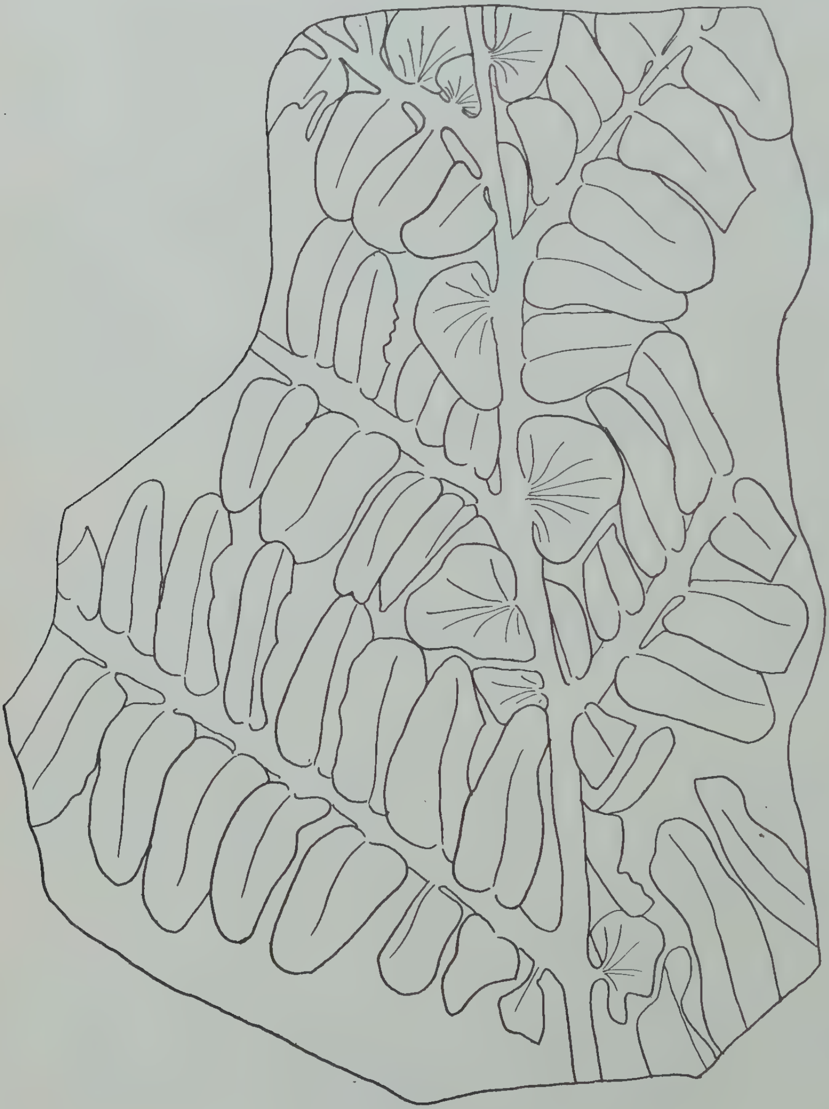
This species occurs in the Transition, Middle, and Lower Coal Measures, but is not common.

NEUROPTERIS VILLIERSII Brongn.

1828. *Neuropteris Villiersii* Brongniart, Histoire des Végétaux fossiles, p. 233, pl. 64. fig. 1.

Schimper (**18**, vol. i. p. 444) considers this species to be the apical portion of a frond, of which *N. auriculata* forms the main portion. Schimper is quite right in his conclusions, for a careful study of the two species shows no characters by which they can be separated specifically. The geological distribution is the same for both.

FIG. 5 *a*.



*Neuropteris auriculata* Brongn. (reduced).

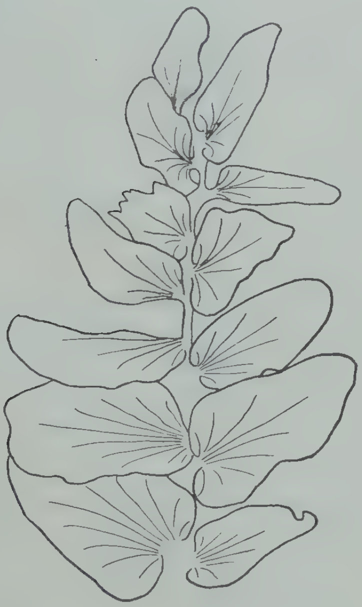
NEUROPTERIS OSMUNDÆ Artis (sp.).

1825. *Filicites Osmundæ* Artis, Antediluvian Phytology, pl. 17.

Careful examination of this species does not show any real differences by which this species can be separated from *N. Villiersii* Brongn. and *N. auriculata* Brongn. It is so similar in character to *N. Villiersii* Brongn. that I do not hesitate to place it with that species as an apical portion of *N. auriculata* Brongn. The shape, size, texture, and venation of the pinnules are the same in both cases.

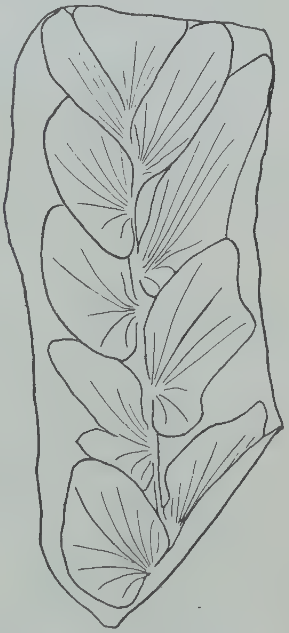
The geological distribution is the same for the three species.

FIG. 5 *b*.



*Neuropteris Osmundæ* Artis (sp.)
(reduced).

FIG. 5 *c*.



*Neuropteris Villiersii* Brongn.
(reduced).

*Conclusions drawn from a critical study of the Species-group* N. AURICULATA.

*N. auriculata* Brongn. was a large frond, bearing numerous cyclopteroid pinnules on a thick rachis, while the apical portions of the frond were of the forms now identified as *N. Villiersii* Brongn. and *N. Osmundæ* (Artis).

The characteristic type of venation, in which most of the veins arise direct from the rachis, entering the pinnule through the broad point of attachment, is a character shared with the genus *Odontopteris*. Potonié (**16**) suggested the name of *Neurodontopteris* for those forms of *Neuropteris* pinnules which show apparent affinities with *Odontopteris*.

### *Characters of Species-group* N. AURICULATA.

The pinnæ have large overlapping pinnules attached to the rachis by a portion of the base, through which many of the veins enter the pinnule after rising in the rachis. In shape the pinnules are broadly oblong with a rounded apex. The veins are moderately fine and numerous.

### *Other species of* NEUROPTERIS.

The following species of *Neuropteris* are remarkable for having either a dentate or crenulate margin, a character which at once distinguishes them from any other species of *Neuropteris*. In no case does this type of leaf-margin appear to be due to a partial decay of the lamina. The species are *N. crenulata* Brongn. and *N. dentata* Lesq., and, although occurring in the British Coal-Measures, they are rare and, when found, are usually in a fragmentary condition. Zeiller (**21**, p. 233, pl. 26. fig. 1; pl. 27. figs. 1–5) gives figures of specimens in which some of the pinnules have entire margins. Until more material has been obtained, I do not think it will be possible to ascertain with any degree of certainty the exact relation existing between these dentate forms and the better-known forms with entire margins.

### CYCLOPTERIS.

Many of the *Neuropteris* fronds had appendages to the rachis which were of a leafy character. These appendages are known as "Cyclopteris." The form of pinnule known as *N. fimbriata* Lesq. was also probably an appendage on the rachis. As Seward (**19**, vol. ii. p. 526) suggests, they may be of the nature of *Aphlebia*. These *Cyclopteris* pinnules have been long known, but as they are usually found detached from the petiole, it is difficult to say to which species of *Neuropteris* the various kinds belong. They vary in size from very small forms 1 cm. or less in diameter up to 10 cm. or more. The venation of these *Cyclopteris* pinnules differs considerably from that of a normal *Neuropteris* in that all the veins radiate from the point of origin of the lamina. This type of venation is seen to a certain extent in some of the pinnules found amongst the species included in the species-group *N. obliqua*. The possession of *Cyclopteris* pinnules, however, is not confined to members of that species-group, as they are found on other species, as, for instance, on the petioles of *N. gigantea* Sternb. in the species-group *N. flexuosa*.

## 5. SUMMARY AND CONCLUSIONS.

As a result of this research it is now possible to state with greater precision the relationships existing between the species of *Neuropteris* commonly found in the British coalfields. The species can be divided naturally into three large groups, each of which has one definite type-species round which the remainder can be grouped. The groups which I call species-groups are identified by the type-species; thus the first group is called Species-group *N. flexuosa.* Although each species-group is distinct from the others, yet they are all connected with each other by species having characters common to two of the groups. These connecting-links or intermediates, which also occur connecting the species within a species-group, have always been a source of trouble to workers on the genus, on account of the difficulty of identification. I suggest, therefore, that the following is the most satisfactory method of identifying these intermediates, as it clearly indicates the two "species" between which they are intermediates —a specimen intermediate between *N. flexuosa* and its varietal form *N. gigantea* would be identified as *N. flexuosa/gigantea.*

Each species-group has its own definite and constant characters by which its members can be identified, but at the same time the members themselves have their own varietal characters, which are subordinate to the characters of the species-group as a whole.

After a careful study of a large number of specimens of *Neuropteris,* I have come to the conclusion that by far the greater number of so-called species are not species in the true sense of the word, but are varietal forms of a very few true species, and are dependent for their characters on their age and position on the rachis and, perhaps, to a certain extent on their environment. The species of *Neuropteris* under discussion appear to be varietal forms of three true species:—*N. flexuosa* Sternb., *N. obliqua* Brongn., and *N. auriculata* Brongn., each of which is the type of a species-group. The false species of *Neuropteris* should, therefore, be identified as forms of the true species; thus *N. gigantea* Sternb. becomes *N. flexuosa* Sternb. forma *gigantea.* This method would give a much clearer idea of the relationships existing between the various forms of *Neuropteris* pinnule.

It has been found that only by ever keeping in mind the facts that age and position are factors which determine the development and structure of each part of the frond, that we can hope to correlate the fragments of pinnæ into an ultimate reconstruction of the whole frond, and thus obtain a clear knowledge of specific identity. I have endeavoured with these facts constantly in mind to sort out and bring into their true relationship most of the common species of *Neuropteris.* Bunbury (7, p. 248) was undoubtedly correct when he said that we are exceedingly liable to create false species from material which originally grew from the same root.

*Geological Distribution of Species.*

| | Upper. | Transition. | Middle. | Lower. |
|---|---|---|---|---|
| *Neuropteris flexuosa* .... | × | × | × | × |
| *N. ovata* .............. | × | × | × | × |
| *N. gigantea* ........... | × | × | × | × |
| *N. tenuifolia*........... | × | × | × | .. |
| *N. macrophylla* ......... | × | × | × | .. |
| *N. Scheuchzeri* ......... | × | × | .. | .. |
| *N. heterophylla* ......... | × | × | × | × |
| *N. rarinervis*........... | × | × | × | .. |
| *N. obliqua* ............. | × | × | × | × |
| *N. callosa* ............. | .. | × | × | .. |
| *N. Schlehani* ........... | .. | × | × | × |
| *N. rectinervis* ......... | .. | .. | × | × |
| *N. auriculata* .......... | .. | × | × | × |
| *N. Villiersii* .......... | .. | × | × | × |
| *N. Osmundæ*............ | .. | × | × | × |

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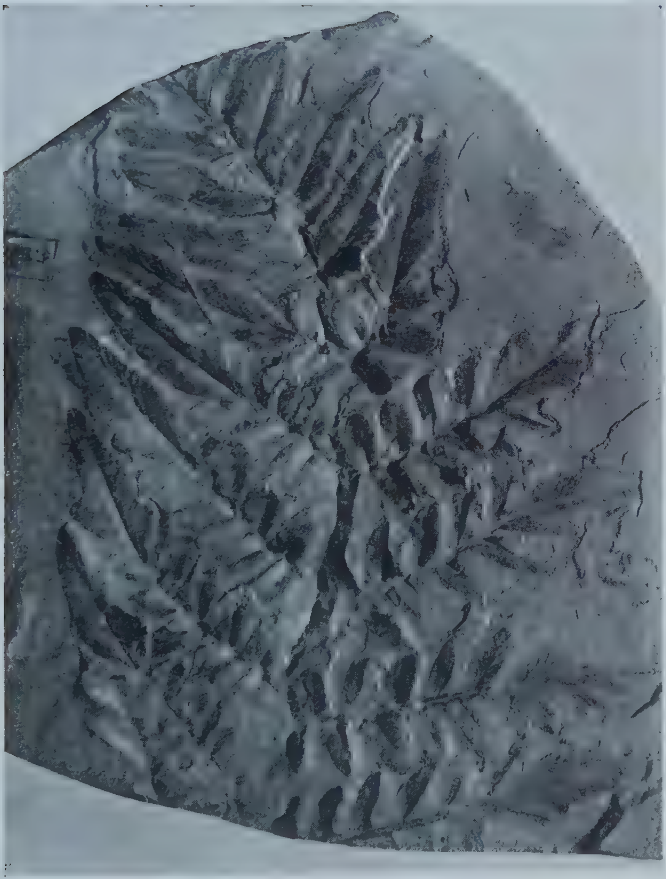

NEUROPTERIS TENUIFOLIA.

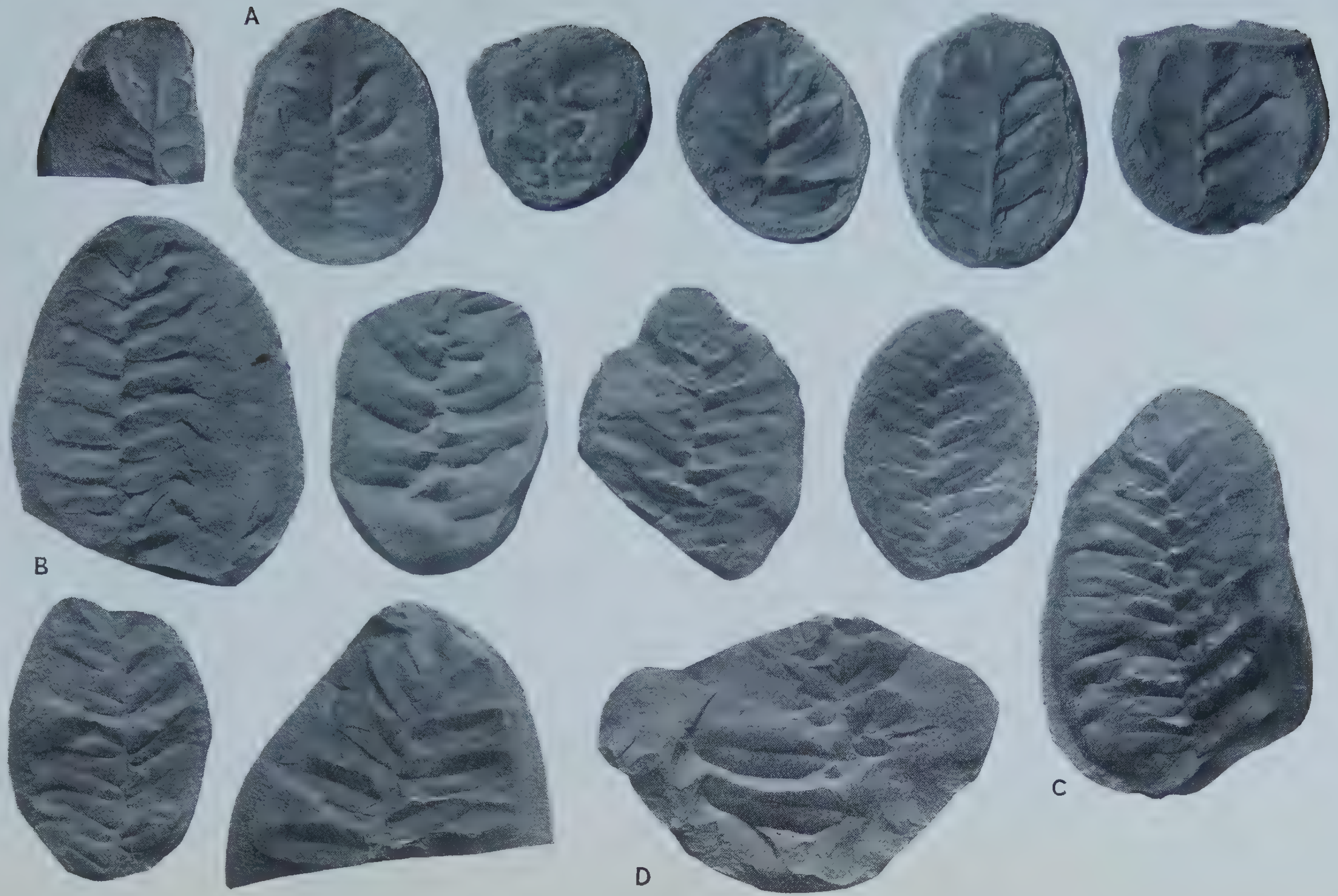

Photo. by J. W. TUTCHER.

SPECIES AND INTERMEDIATES OF NEUROPTERIS FLEXUOSA.

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## EXPLANATION OF THE PLATES.

### PLATE 5.

A specimen of *Neuropteris tenuifolia* Schloth., with some of the pinnate lateral pinnæ, showing the characters usually associated with *N. flexuosa* Sternb. × 0·09.

### PLATE 6.

A series of specimens from Crawcrook, showing species and intermediates belonging to the Species-group *N. flexuosa*. × 0·66.

A.—*N. flexuosa* Sternb.; B.—*N. gigantea* Sternb.; C.—*N. tenuifolia* Schloth.; D.—*N. macrophylla* Brongn.

The rest of the specimens are intermediates; those in the top row being intermediates between A and B; those in the second row between B and C, and those in the bottom row between C and D.

# On the Seedling Structure of *Tilia vulgaris* Heyne.

By H. S. Holden, D.Sc., F.L.S., and S. H. Clarke, B.Sc., University College, Nottingham.

(With 20 Text-figures.)

[Read 19th November, 1925.]

Although *Tilia vulgaris* flowers freely in England it is apparently uncommon for it to set any appreciable number of good seed. A few, however, are produced each year by a small group of trees in the vicinity of University College, Nottingham, as a careful search usually yields one or two seedlings *. The spring and summer of 1923 seem to have been exceptionally favourable for the ripening of the seed, as in the spring of 1924 upwards of seventy seedlings were collected ; it is upon these that the present account is based.

## Morphology.

The structure and germination of the seed and the morphology of the seedling have been described and figured by Lubbock (**9**), and figures of the seedling are also given by Marshall Ward (**16**) and by Kerner (**8**). The cotyledons are epigeal and thinly pubescent, and are typically five-lobed. We may conveniently designate the lobes as the median, intermediate, and lateral lobes respectively. It is a point of some interest to note that there is quite a considerable variation in the proportion of the lobes one to another and in minor features also. Among the specimens collected at Nottingham the commonest type, which may be referred to as the mean type, is shown in fig. 1. It will be noted that the median and lateral lobes are somewhat larger than the two intermediate ones and that all are somewhat obtusely pointed. From such a mean type a graded series of variants may be derived, two extremes of which are illustrated in figures 2 and 3. In the first of these the variation consists in the elongation of the lobes which have consequently become more acute, whilst in the second the whole cotyledon has undergone compression so that the lobes are relatively short and stumpy. Occasionally, some degree of asymmetry is produced by inequalities in the lobing. One such case is shown in fig. 4, in which the intermediate lobe on the right is much smaller than its fellow, whilst in a second case (fig. 5) there appears to have been a partial fusion of the apical lobe and the left intermediate lobe. This second specimen is also interesting on account of the lobes having rounded apices instead of the more normal pointed ones. In addition to the variation in the size of the main lobes the development of subsidiary lobes both on the median and lateral lobes may be noted. Fig. 6 shows their symmetrical development on both, whilst in fig. 7 an example of their development on the central lobe only is shown. They may be little more than slight outgrowths of the lobe-margin as in the asymmetrical case shown in fig. 8 *a*, or be strongly developed as shown in fig. 9. There is no indication of co-ordination between the two cotyledons of the same seedling in the development of the accessory lobes, though where they are well developed in one they are at least represented in the other. A small accessory lobe on one lateral lobe is shown in Lubbock's figure (**9**, fig. 223), whilst they are well developed on all the lateral lobes of the seedling figured by Marshall Ward (**16**, fig. 159). Kerner's figure shows a slight one on one of the median lobes only (**8**, fig. 148).

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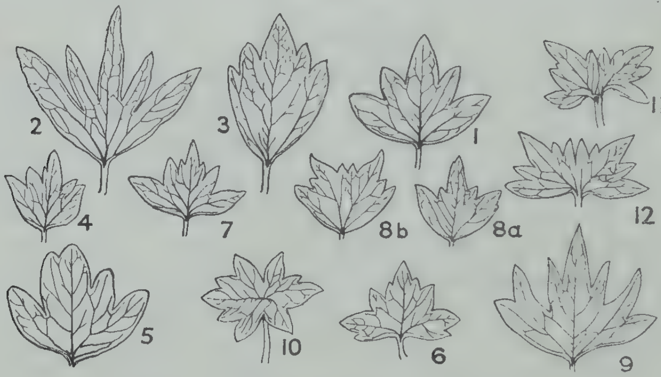
* Specimens from these trees have been deposited in the Botany Department of the British Museum (Natural History).

As frequently happens when a large series of seedlings is collected, a few specimens exhibiting some degree of abnormality were obtained; these included both syncotyls and polycotyls. Of the latter, one (fig. 10) was amphisyncotylous and showed suppression of an intermediate lobe in one cotyledon, whilst two others (figs. 11, 12) showed unilateral syncotyly which had resulted in the reduction of the lobes on the symphysis side. The polycotyls were two in number, namely a hemitricotyl and a tricotyl, the cotyledonary members of the former being shown in figs. 8 *a*, 8 *b*.

Figs. 1–12.



Variations in the morphology of the cotyledons.

## Histology.

The surface hairs clothing the seedling are of two kinds and show well-marked differences in distribution. Most of them are unicellular and end in an acute point (fig. 13), though occasionally a single transverse wall may be present. The hairs of this type are scattered over the hypocotyl, but in the cotyledons they are confined to the areas over the veins and to the petioles. Each arises as an epidermal outgrowth, but those on the upper surface differ from those on the lower surface in being surrounded by cells which form a slightly raised area (fig. 14). The base of the hair in many cases appears to be practically square when seen in plan, but in other cases it is elongated in the direction of the path of the vein over which it lies (fig. 15). The walls are slightly lignified and give a pink reaction with phloroglucinol after acidification with hydrochloric acid.

The second type of hair, which is multicellular and club-shaped (fig. 16 *a*), is much less abundant and only occurs on the upper surfaces of the cotyledons *between* the veins and on the inner faces of the cotyledonary petioles. Each consists of a relatively stout stalk composed of two or three superposed cells above which is a central region showing four cells in transverse section (fig. 16 *b*). Succeeding this is a two-celled region (fig. 16 *c*), which in turn is capped by a single cell. This may be either practically hemispherical or broadly wedge-shaped with a convex free surface.

Figs. 13–16.

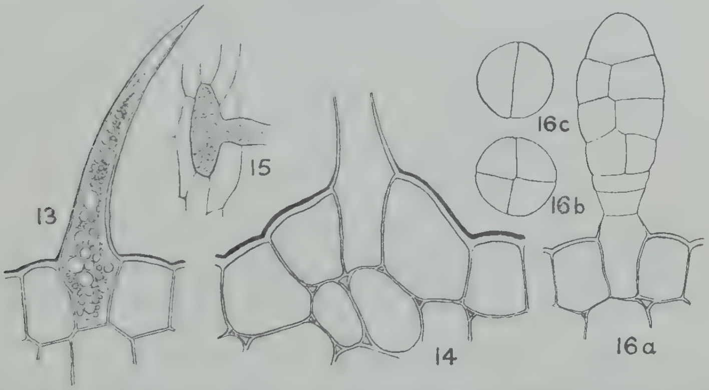


Fig. 13. A pointed unicellular hair from the lower epidermis of the cotyledon; the majority are considerably longer than the one figured. Fig. 14. Base of a hair from the upper epidermis of the cotyledon, to show the larger epidermal cells and the slightly raised area surrounding the hair. Fig. 15. Elongated base of a hair in surface view. Fig. 16 *a, b, c*. Club-shaped hair in longitudinal and transverse sections. The cell-contents of the hairs, which are similar in all, are only shown in fig. 13.

The cells of both types of hair are crowded with bright yellow globules of all sizes (fig. 13). These have the appearance of oil-drops, but do not give the reactions characteristic of fatty substances. They are insoluble in alcohol, chloroform, ether, and xylol and are unaffected by either acids or alkalis. We have been unable to determine their precise nature, but their resistance to the action of solvents is a point of some interest.

The cells of the upper epidermis are polygonal in surface view, those over the veins being compressed laterally. They are distinctly larger than those of the lower epidermis (*cf.* figs. 13 & 14). The walls of the latter are sinuous in character (fig. 17 *a*) except for those below the veins, which resemble the cells similarly situated on the upper surface. The stomata are confined to the under surface and are remarkable for their variation in size. Two chief types are recognisable, the first of which is relatively large and is ovoid in plan, whilst the second is much smaller and is almost circular in plan (fig. 17 *a*) Among the smaller type a few examples of twinned stomata have been observed, one of which is shown in fig. 17 *b*.

Scattered through the cortex of the cotyledonary petioles and of the hypocotyl and roots are cells containing mucilage, these standing out clearly after staining.

FIG. 17.

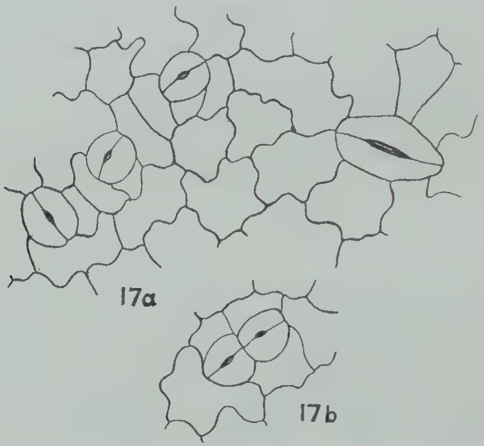


Fig. 17 *a*. Portion of the lower epidermis from the cotyledon, to show the variation in the size of the stomata. Fig. 17 *b*. The same showing twinned stomata.

The yellow fat-like globules occurring in the epidermal hairs, to which reference has already been made, are abundant in the bundle-sheath and the adjacent layers of the hypocotyl, petiole, and root, and are also present in the medullary parenchyma. They are rare or absent in the cortical cells.

## THE VASCULAR SYSTEM.

The midrib of the cotyledon is a collateral bundle which becomes somewhat extended tangentially following its junction with the bundles from the intermediate lobes. This increase in width becomes more pronounced as a result of the incoming of the strands supplying the lateral lobes. The union of the laterals with the midrib may occur at or near the base of the lamina or at various levels in the petiole. In the composite bundle thus produced, although the phloem forms a continuous mass, it is possible in young seedlings to differentiate the midrib xylem from that of the lateral lobes (figs. 18, 19, 20), although this becomes impossible in older seedlings. The characteristic triad structure, with its central file of xylem elements flanked by separate phloem groups, is not shown in the petioles of even the youngest seedlings examined, the phloem being continuous. A very frequent feature in the upper part of the hypocotyl is one in which the metaxylem, as seen in transverse section, forms two fan-shaped masses, one on either side of the protoxylem. Occasionally the metaxylem elements nearest the protoxylem curve over this and, in the younger seedlings, as a result, isolated metaxylem vessels may be seen above the protoxylem in the cotyledonary plane (fig. 20).

Figs. 18–20.

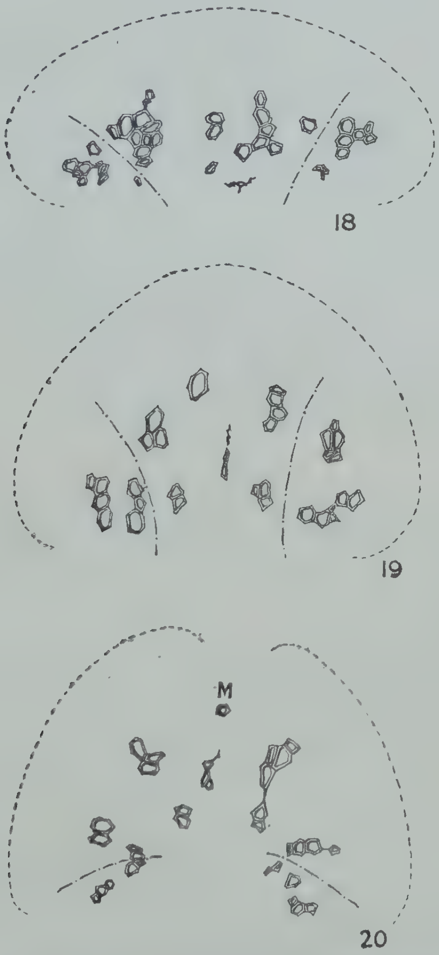


Fig. 18. Transverse section of the cotyledonary midrib after union with the lateral strands. Fig. 19. The same at the top of the hypocotyl. Fig. 20. The same in the middle of the hypocotyl. Note the isolated metaxylem element (M) above the disorganising protoxylem in the cotyledonary plane. Xylem only shown, phloem indicated by plain dotted line, junction of lateral strands and midrib indicated thus –.–.–.–

The epicotyledonary strands play no significant part in transition. As is the case in the Sycamore (*Acer Pseudoplatanus*) (**13**) the behaviour varies, the types noted being as follows:—

1. The phloem bifurcates and unites with that from the cotyledons, whilst the xylem dies out *in situ.*

2. Both phloem and xylem divide and unite with the corresponding elements from the cotyledons.
3. The strand moves as a whole to unite with the cotyledonary strand.

The transition to typical tetrarch root-structure is extremely leisurely. The lateral xylems separate from those of the midrib (fig. 20) more and more widely and finally unite in the lower half of the hypocotyl. Here they develop groups of protoxylem and form typical secants in the intercotyledonary plane. Actual root-structure is only attained some distance below the collet. A small medulla is present throughout the root.

Although the sequence described above holds good for the majority of the seedlings examined a number of interesting variations have been encountered. The simplest of these, and one which does not in any way affect the root-structure, is produced by the complete independence of the lateral veins which at no part of their course come into contact with the midrib bundles. This type of transition, which occurs only in one seedling, is typical of many other species such, for example, as *Impatiens Roylei* (**10**, **11**).

A second variant, also represented by one seedling only, has resulted from a condition directly opposite to that described above. In this second case the lateral strands of one side in each cotyledon become completely merged with the midribs and do not again separate. The result is that triarchy obtains in the root, two of the poles being derived from the midribs and one from the two laterals which behave normally. The transition phenomena in this seedling are reminiscent of those described by Compton (**3**) for *Dorycnium hirsutum*, allowance being made for the fact that the latter is a species with independent lateral strands.

Still a third variant, in this case represented by two seedlings, is one in which the root is pentarch. In one of these seedlings the earlier part of the transition is quite normal. Following the complete separation of the laterals, however, the two on one side, instead of uniting, continue down the hypocotyl as independent collateral strands. These gradually flatten out to form tangentially extended plates and, just above the collet, develop separate protoxylems in an exarch position. The phloems bifurcate just prior to the appearance of the new protoxylems, and form typical groups by lateral union with adjacent groups. The second example is one in which the whole of the transition to root-structure is perfectly normal, so that the root is primarily tetrarch. In the lower portion of the root, however, a small group of metaxylem vessels becomes separated off from one of the intercotyledonary poles and moves laterally. The phloem group which overarches it then divides and an exarch protoxylem is developed opposite the gap thus formed, so producing a pentarch condition. It seems reasonable to regard this second example as one in which the independence of the laterals as pole-forming units is asserted relatively late in the transition, so that its difference from the first example is one of degree rather than kind.

With regard to the abnormal seedlings, only one of the syncotyls showed any vascular abnormality, this being the one in which the unilateral syncotyly was most marked. As a result of compression the vascular strands supplying the lateral lobes on the symphysis side unite with the midribs precociously. This union is permanent so that only the two midribs and the second pair of laterals form poles, the root as a consequence being triarch.

The hemitricotyl (fig. 8 *a*, *b*) and tricotyl were both pentarch, but in these seedlings the pentarchy has a totally different origin from that occurring in the dicotyl described in an earlier portion of this paper. In both cases the midrib strands each formed a root-pole, the two remaining poles being produced by the lateral strands. These in one cotyledon behaved quite normally, separating from the compound central strand and uniting with similar laterals from the adjacent cotyledons, thus producing two further poles. In the tricotyl the suppression is due to the complete merging of one of the laterals in each of two cotyledons with the midrib. In the hemitricotyl the adjacent lateral lobes along the line of junction of the two imperfectly separated cotyledons are not developed and, as a consequence, the lateral strands which would normally supply them are non-existent.

## Discussion.

Although a considerable body of work on seedling anatomy has now accumulated it has not yielded the clearly defined information regarding phylogeny which it was hoped would accrue. All the same a number of interesting results have been obtained, and it is reasonable to assume that with the continued pursuit of seedling investigation a satisfactory conception of the features which characterized the ancestral types will be possible. Dr. Miles Thomas has already summarized certain aspects of her extended period of work in a recently published report (**15**), and her fuller account will be looked for with considerable eagerness. One fact which does emerge more or less clearly is that the variations in seedling anatomy are due not to any great number of fundamentally different basic types, but rather to a ringing of the changes on the components of a common group of vascular strands. The constituents of this common group, the chief of which are the cotyledonary midrib and its laterals, may undergo, in different seedlings, various changes with regard to linkage, fusion or independence, and in relative importance or position. Where, as sometimes happens, a new factor such as the epicotyledonary strands plays an important part a further series of variations is rendered possible (**7**).

Undoubtedly the commonest type of vascular arrangement in tetrarch seedlings is that in which the midrib and its laterals remain independent. The opposite condition in which they constitute a compact median compound strand is much less frequent. It has been recorded and briefly described by Miles Thomas (**14**) for *Althæa*, and by De Fraine for *Opuntia* and *Nopalea* (**6**).

*Tilia* furnishes an example of an intermediate condition since, although the fusion of the phloem system of the median and lateral strands is complete, the union of the xylem strands is relatively loose and is rather in the nature of a close linkage than a merging of identity. The fact that *Tilia* may exhibit a type of transition in which the laterals remain independent throughout is worthy of note in this connection. Such a condition is relatively rare in *Tilia*, but other species such as *Pyrus communis* (**14**) show a large degree of variability. *Tilia* shows some approach to *Pyrus communis* also in the fact that the laterals may assume a more important role in root-pole formation, each forming a pole independently instead of uniting to form a common pole. In *Tilia* the condition is unilateral so that pentarchy results, whilst in *Pyrus* both sets of laterals may be involved, thus leading to a hexarch root condition.

Miss Bexon, who has recently made an intensive study of *Althæa* (**1**), has shown that in this case also a considerable amount of variation occurs producing a tetrarch-hexarch range in the root, so that in the case of that genus a more extended comparison with *Pyrus* is possible.

The reverse condition, in which a reduction from tetrarchy to triarchy occurs, is frequent in the Leguminosæ, and Compton (**3**) interprets this with some degree of probability as illustrating a tendency towards reduction to diarchy from an ancestral tetrarch condition.

It is remarkable that, in *Tilia*, such a reduction may occur in what appears to be an absolutely normal seedling, and this renders one less confident in ascribing to compression the loss of a pole in the syncotyl described earlier. At the same time there is a considerable body of evidence (**4, 10, 11,**) that the compression consequent on unilateral syncotyly does lead to a lessening of the importance of the lateral strands on the symphysis side, and it may be that in *Tilia* a rarely expressed potential reduction is rendered more frequent by such a compression.

We are perhaps on safer ground in ascribing the suppression of one of the intercotyledonary poles of the tricotyl to crowding, as it is characteristic of the majority of polycotyls to find the number of poles reduced from what one would expect by comparison with the normal seedling.

In an earlier paper on polycotyly (**12**) it was suggested that the division of the meristem which resulted in the hemitricotylous and other polycotylous states might be either qualitative or quantitative. If the former, the midribs of the two resultant cotyledons would behave in transition like a single normal midrib; if the latter, then each of the daughter midribs would show triad structure and exhibit a certain degree of independence in transition. If this conception is sound, the hemitricotyl and tricotyl of *Tilia* described above both have resulted from an apical division of the quantitative type.

## SUMMARY.

1. The seedling of *Tilia vulgaris* possesses two typically five-lobed epigeal cotyledons.

2. The cotyledonary lobes vary in size and may show elongation or shortening compared with a common mean type. They may also develop accessory lobes.

3. The aerial parts are thinly pubescent, the hairs present being of two types:—(*a*) Unicellular ones confined to the epidermal ridges above and below the veins of the cotyledon laminæ but generally distributed over the hypocotyl. (*b*) Club-shaped multicellular hairs confined to the upper surfaces of the cotyledons between the veins.

4. The vascular system is tetrarch in plan and typical root-structure is only attained some distance below the collet.

5. Seedlings showing triarchy or pentarchy also occur.

6. Syncotylous seedlings, where the syncotyly is unilateral and at all pronounced, show triarch symmetry.

7. The polycotylous seedlings examined are pentarch, though the pentarchy occurring in this case is not homologous with that occurring in dicotyls.

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# Chromosome Studies in *Tulipa* and some related Genera.

By W. C. F. Newton, B.Sc., F.L.S.

(Plates **7–10** and 1 Text-figure.)

[Read 2nd April, 1925.]

The development of the embryo-sac and the process of fertilization in certain tulips have been studied by Guignard (1900), Ernst (1901), Schniewind-Thies (1901), and Strasburger (1908), but none of these authors has paid special attention to the chromosomes. Guignard studied three species which he describes as *Tulipa Celsiana* (probably *T. australis* Link), *T. sylvestris* Linn., and *T. Gesneriana* Linn. In all these he found twelve to be the reduced number of chromosomes. I have only been able to obtain the "*forma major*" of *T. sylvestris* which has twenty-four as the reduced number, so that it seems possible that this species exists in both diploid and tetraploid forms.

Guignard found that there was an anomaly in the development of the embryo-sac in *T. sylvestris* and *T. Celsiana*. There was no definite polarization of the three successive divisions in the sac and the eight nuclei produced all lay towards its upper end. The embryo-sac was very broad in proportion to its length, and there was a large vacuole at the chalazal end instead of in the middle between the two nuclei produced by the first division, as is usual. Later there was no definite egg apparatus, but the polar nucleus was distinguishable by its greater size and its position nearer the antipodal end of the sac. In *Tulipa Gesneriana*, a name applied to various horticultural varieties, Guignard found that the development of the embryo-sac was like that in *Lilium*, a view with which Ernst and Strasburger agree, the latter adding the observation that the number of chromosomes in the chalazal nucleus after the first division may become doubled.

In the present investigation the early development of the embryo-sac has been examined in a considerable number of species, and the results are of some interest in connection with the classification of the species. Boissier divided the genus into two sections, namely, Leiostemones, characterized by glabrous filaments, and Eriostemones, in which there is a tuft of hairs at the base of the filaments. The development of the embryo-sac has been followed in eight species of the latter section, and in all it resembles that described by Guignard for *T. Celsiana* (*australis* Link). This unpolarized type of sac may therefore be regarded as characteristic of the Eriostemones including *T. dasystemon* and its allies, which are sometimes shifted to a separate subgenus on account of the style-like upper sterile portion of the ovary. No doubling has been observed in any embryo-sac of the unpolarized type. Eleven species of the Leiostemones selected to include the most widely different species have been found to agree in having an embryo-sac of the polarized *Lilium* type, but great diversity exists with regard to the doubling of the chromosome number in the daughter nuclei of the first meiotic division. No doubling was found in *T. Clusiana* DC., *T. præstans* Hoog., or in *T. viridiflora* Baker. In the individuals examined of *T. Kolpakowskiana* Regel, doubling was found in every sac which was countable, but in two instances it occurred at the micropylar end and not at the chalazal end. This type of doubling would lead to the production of a diploid egg, and on fertilization to a triploid embryo. The triploids, *e. g.* Keiserkroon, Massenet, which occur among the horticultural varieties have probably arisen in this way as no tetraploids have been formed.

Sargant (1896) observed that in *Lilium Martagon* doubling occurred in every embryo-sac in which she was able to obtain a count, but Strasburger, in the species examined by him, found there was no doubling in the earlier flowers though it occurred in the later ones in the same raceme. In view of the complexity of what occurs in *Tulipa* together with the small number of counts that can be obtained from any one ovary, much further work will be required before the significance of the difference of behaviour in the different species examined can safely be estimated. Strasburger thought that the doubling in the chalazal nucleus might be the result of the better nutrition at that end of the sac, but, in view of the occurrence of doubling at the micropylar end only, this hypothesis is untenable. The increase in number of the chromosomes occurs, however, too frequently and too regularly for it to be regarded as strictly comparable to the doubling that not infrequently occurs in somatic tissue. The determination of the method by which the doubling takes place is rendered difficult by the fact that in any given sac one cannot be sure whether it is going to take place or not. Prophases of the second division have been seen in which the doubling has quite clearly occurred, but all anaphases of the first division that have been seen have been normal. The final settlement of the questions raised by the observations reported in the present paper will require the examination of much more material, an examination which will be undertaken as soon as possible.

*Material.*—I am indebted for most of the *Tulipa* material used and for the identification of the species to the late Mr. W. R. Dykes, who was kind enough to place his very extensive collection and knowledge of the genus at my disposal. The appended list gives the diploid chromosome number of the species examined, the haploid number where it has been determined separately being added in brackets. The chromosome numbers of material examined for purposes of comparison are also given if they have not been previously published.

## TULIPA.

### Leiostemones.

| | |
|---|---|
| Tulipa Batalini Regel | 24 |
| T. Maximowiczii Regel | 24 (12) |
| T. linifolia Regel | 24 (12) |
| T. stellata Hooker | 48 |
| T. chrysantha Boiss. | 48 (24) |
| T. Clusiana DC. about | 60, $(24_{11}, 12_1)$ |
| T. Kolpakowskiana Regel | 24 (12) |
| T. Greigi Regel | 24 |
| T. Eichleri Regel | 24 |
| T. Kauffmanniana Regel | 24 (12) |
| T. præstans Hoog. | 24 (12) |
| T. Sprengeri Baker | 24 |
| T. armena Boiss. | 24 |
| T. galatica Freyn. | 32 |
| T. viridiflora Baker | 24 (12) |
| Copper colour (hort.) | 24 |
| Keiserkroon (hort.) | 36 |
| Massenet (hort.) | 36 |
| Murillo (hort.) | 24 (12) |
| Duc van Thol (hort.) | 24 (12) |

### Eriostemones.

| | |
|---|---|
| Tulipa dasystemon Regel | 24 (12) |
| T. humilis Herbert | 24 (12) |
| T. pulchella Fenzl | 24 |
| T. biflora Pall. | 24 |
| T. turkestanica Regel | 24 |
| T. primulina Baker | 24 (12) |

### Eriostemones (*cont.*).

| | |
|---|---|
| Tulipa australis Link | 24 (12) |
| T. sylvestris Linn. | 48 (24) |
| T. orphanidea Boiss. | 24 (12) |
| T. Whittalli Elwes | 48 (24) |
| T. Hageri Heldr. | 24 (12) |

## FRITILLARIA.

| | |
|---|---|
| Fritillaria Meleagris Linn. | 24 (12) |

## LILIUM.

| | |
|---|---|
| Lilium tenuifolium Fisch. | (12) |
| L. pyrenaicum Gouan | (12) |

## LLOYDIA.

| | |
|---|---|
| Lloydia serotina | 24 |

## CALOCHORTUS.

### Macrodenus.

| | |
|---|---|
| Calochortus albus Dougl. | 20 (10) |
| C. amabilis Purdy | 20 (10) |
| C. Benthami Baker | 20 (10) |
| C. Maweanus Leichtl. | 20 |

### Mariposa.

| | |
|---|---|
| Calochortus Plummeræ Greene | 18 |
| C. clavatus S. Wats. | 16 |
| C. Catalinæ Watson | 14 (7) |
| C. lutea Douglas | 14 |
| C. venusta Benth. var. Eldorado | 14 (7) |
| C. Vesta Purdy | 28 (14) |

*Chromosome Number and Form.*—In the genera *Lilium*, *Fritillaria*, *Erythronium*, and *Tulipa* no exception to the haploid chromosome number twelve has been previously reported, but *Lilium* is the only genus in which any considerable number of species has been examined. The mode of attachment and the comparative size of the chromosomes have been adequately figured by Navashin (1914) for *Fritillaria tenella*, in which plant three types of chromosome occur. The longest have sub-median attachment, the shortest terminal, while those of intermediate size have sub-terminal attachment and constrictions. In *Erythronium* the same three classes can be distinguished in the figures of Schaffner (1901), while in *Lilium* many authors have described and figured diverse attachments without, however, giving a detailed account. Three types of chromosomes can also be recognized in all the species of *Tulipa* that I have examined in which the chromosome number is twelve or a multiple of twelve. In Pl. **8**. fig. 10 anaphase chromosomes, drawn with the help of a camera lucida, have been traced and arranged so as to facilitate the comparison of the different species. The conditions present in the Eriostemones and the greater number of the Leiostemones are represented in fig. 10, *a, b* and *c*. The chromosomes of type I, in which the attachment is sub-median, are very little or not at all longer than those of type II, in which the attachment is sub-terminal. In this respect there is a difference from *Lilium* and *Fritillaria,* in both of which the chromosomes of type I. are decidedly the longest. This is also the case in two species of *Tulipa* which have been examined, *T. galatica* and *T. armena* (fig. 10, *d* & *e*). The chromosomes of type III, the shortest, differ from those of *Fritillaria Meleagris* (and of *F. tenella* Navashin (1914)) in that the attachment is subterminal instead of terminal. The *Lilium* species that have been examined resemble *Tulipa* in this respect. In *Lilium* and *Fritillaria* and in *Tulipa*, with the exception of the five species mentioned below and the tetraploid series, there are two, and only two, pairs of chromosomes with sub-median attachment. *Tulipa linifolia* (Pl. **8.** fig. 10 *f*), *T. Maximowiczii,* and *T. Batalini* are alike in the fact that all their chromosomes have terminal attachment with a constriction so close to the end that the proximal segment is spherical. They are also peculiar in each having a single pair of very short chromosomes. The longest chromosomes number two pairs and may correspond to type I. of the other species. Types II and III are not to be distinguished, while the small pair represents a new differentiation. The chromosomes are all much smaller than those of the species described above, as are also the nuclei and the cells. *Tulipa Clusiana* (Pl. **8.** fig. 10 *g*) has chromosomes like those of *T. linifolia*, but the species is pentaploid. The cells and nuclei are between three and four times the volume of those of *T. linifolia,* but the plant, if a little taller, is more slender. In *Tulipa* there is, except in diploid and tetraploid forms of the same species, no positive correlation between somatic size and the number of chromosomes or the size of the cells. There are two series of species, one with large and one with relatively small chromosomes. Within each of these series there is positive correlation of chromosome number and nuclear size, but somatic size is quite independent. *Tulipa linifolia, T. Maximowiczii*, and *T. Batalini* form a natural group distinguished by cytological as well as by their morphological characteristics. *T. stellata* and *T. chrysantha* are tetraploid forms, probably not specifically distinct, which have probably had a part in the origin of the pentaploid hybrid *T. Clusiana. T. Whittalli* is a tetraploid form standing in a similar relation to the plexus of forms grouped under the name of *T. orphanidea*, to that in which *T. sylvestris* stands to *T. australis* and its allies.

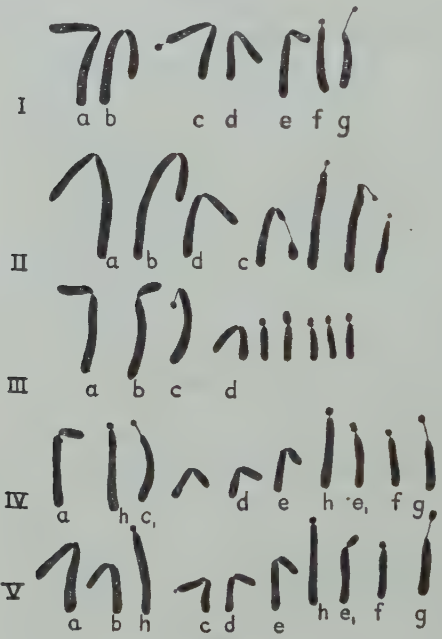
The chromosomes of *T. Kolpakowskiana* (Pl. **8.** fig. 10 *h*) are in respect of size intermediate between those of *T. linifolia* and the normal type for the genus. There are no chromosomes with sub-median attachment (type I), but the constrictions are further from the ends of the chromosomes than in *T. linifolia,* and there is no exceptionally small pair. So far I have found no other species with chromosomes resembling those of *T. Kolpakowskiana.*

The chromosomes of *T. galatica* Freyn. are shown in metaphase (Pl. 7. fig. 9) and the different types of chromosome are shown as they appear in anaphase (Pl. 8. fig. 10 *d*). This species is very similar to *T. armena* Boiss., from which it differs principally in having yellow instead of red flowers. The chromosomes of *T. armena* are shown in fig. 10 *e*. *T. galatica* agrees with *T. armena* in that the chromosomes of type I. have more nearly equal arms than any other species I have examined. It differs in having sixteen instead of twelve pairs of chromosomes, four pairs being very small. These small chromosomes are not represented in any member of the Tulipeæ at present described; and, given the very great similarity of *T. galatica* and *T. armena*, the possibility of their having been introduced from some cross outside the genus may be neglected. There can be no doubt that they have arisen by the fragmentation of some of the chromosomes of a complement like that of *T. armena*. There has not been a complete reorganization of the chromatic material as the chromosomes of type I. have remained unaffected.

Cases of fragmentation or fusion of chromosomes have been reported from many genera, and usually it has been a matter of doubt which has occurred. In the present example the fact that twelve is the basic number of all the other species of the genus as well as of those of the most closely related genera, makes it certain that it is fragmentation which has taken place. In the family Liliaceæ itself Gates has suggested that the great disparity in the sizes of the chromosomes of *Yucca* is due to a process of fragmentation; but in view of the fact that alterations in relative size may have occurred without any change in number (cf. *T. linifolia*), and also because there are no closely related plants with lower numbers with which to compare the species in question, it is only justifiable to say that fragmentation is one of the ways by which the chromosome complement of *Yucca* might have arisen. Metz (1916) has described a series of species of *Drosophila* in which the chromosome numbers are six, eight, ten, and twelve. He has suggested that sometimes, at least, the difference in number depends upon the separate existence of rod-shaped chromosomes with terminal attachment or their union by pairs into V-shaped chromosomes with median attachment. Similar ideas have been put forward by Robertson (1916) to explain the difference of three in the chromosome numbers between the species of the orthopteran genera *Syrbula* and *Chorthippus*. In the latter genus the arms of the three V-shaped chromosomes are said to correspond in size with six of the straight chromosomes of *Syrbula*. These authors emphasize the occurrence of a constriction at the apex of the V as an indication of the compound nature of the chromosome. This argument cannot be regarded as convincing since most, if not all, chromosomes exhibit a constriction at their point of attachment. The small chromosomes of *Tulipa galatica* have in each case a constriction which must have been developed subsequent to their becoming independent units. By way of analogy the attachment constriction may be regarded as a kind of centre of gravity of the chromosome, the position of which depends on the structure of the chromosome and also on its existence as an independent unit.

In *Tulipa* there is only a single departure from the basic number twelve, while no deviation from that number has been met with in the genera *Fritillaria*, *Lilium*, *Lloydia*, or *Erythronium*. It is quite otherwise with *Calochortus*, the remaining large genus included in the tribe Tulipeæ. This genus was divided by Baker into two main sections, Macrodenus and Mariposa. In the former the basic chromosome number is ten; in the latter I have so far found the numbers seven, eight, nine, and fourteen. The types of chromosome found in a number of species of the genus are arranged in order to facilitate comparison in text-figure 1. In the uppermost row, lettered from *a* to *g*, are given the seven chromosomes which form the haploid complement of *Calochortus Catalinæ*. It will be seen that each is easily distinguishable from the others by size, attachment, the possession of trabants, or by a combination of these characters. In some individuals of *C. Catalinæ* examined, one member of the pair *c* possessed the trabant

Text-fig. 1.



Haploid complement of chromosomes of certain species of *Calochortus*. I. *C. Catalinæ*. II. *C. venusta* var. *Eldorado*. III. *C. Plummeræ*. IV. *C. amabilis*. V. *C. Benthami*. The lettering indicates the homologies suggested.

and in the other it was missing. The chromosomes of *C. venusta* var. *Eldorado* are shown in row 2 of the figure. Here chromosome *c* differs from the corresponding one in *C. Catalinæ* in that the trabant is longer and the arm which bears it proportionally shorter. The chromosome complement of *C. lutea* is exactly similar to that of *C. venusta*. *C. Vesta*, on the other hand, has a complement exactly like that of *C. Catalinæ* but doubled, a surprising result since in external morphology it is much more similar to *C. lutea* and *C. venusta*. The third row represents the nine chromosomes of *C. Plummeræ*. The first four may be homologized with *a*, *b*, *c*, *d* of *C. Catalinæ*. The remaining five, all very small, cannot be recognized in any other species. It is possible that they have arisen by fragmentation, but the species with eight, nine, and ten chromosomes do not represent progressive stages of a single process. The fourth and fifth rows in the figure represent the chromosomes of *C. amabilis* and *C. Benthami*, examples respectively of the "Globe" and "Star" tulips united in the section Macrodenus. There is general agreement between the chromosomes of the two species, but differences of attachment distinguish types *a* and *c*. In *C. Benthami* all the types present in *C. Catalinæ* can be recognized, indicating that in this case there is no question of increase in number through fragmention, but the increased number may result from crossing followed by the doubling of certain chromosomes such as has been described by Clausen in *Viola*.

The genus *Calochortus* was placed in the Tulipeæ with some hesitation. The very considerable cytological differences from the other genera, which are so uniform among themselves, emphasize the desirability of giving it a separate standing. At the same time I should not advocate such a removal on cytological grounds alone. The differences between *Tulipa* and *Calochortus* are very similar in kind to those that distinguish *Hyacinthus* from *Muscari*. There is as yet no evidence that morphological changes in the chromosomes are in any way proportional to the actual changes in their properties, while a glance down any list of chromosome numbers is sufficient to dispel a tendency to give these an exaggerated importance.

*The Reduction Divisions.*—The reduction division in the megaspore mother-cells in those tulips which I have examined, takes place within a few days of the opening of the flower, or occasionally after the flower has opened. The reduction in the microspore mother-cells takes place in many species in late summer, and from September to the end of March there is a constant succession of species undergoing reduction. The development of the anthers goes on during the resting stage of the bulb. There is no exact correlation between the earliness at which the reduction takes place and earliness of flowering. *Tulipa armena* and *T. linifolia* flower about the same time, both being late species, but the former has completed its reduction divisions by the end of September, the latter not until the end of March. In tulips of the same variety grown together under the same conditions there is very little difference in the time at which reduction takes place, and within two or three days of the finding of the first divisions nothing but tetrads are to be found, however many bulbs be sacrificed. As an example, on October 20th four flowers of *T. primulina* were examined and all were in the later zygotene stage of fig. 21 (Pl. **9**). Two days later four more flowers were examined and showed in three cases all stages from diplotene to the completion of the second division, while in the fourth nothing but tetrads was found. This characteristic allows of a fairly accurate estimate of the duration of the more lengthy stages in reduction.

*Methods.*—Three stamens from each flower examined were immediately placed in the fixing fluid, various modifications of Flemming's fluid with reduced acetic acid being used. The remaining anthers were teased out into fixing fluid and afterwards stained under the cover-glass with toluidene blue, dehydrated and mounted in Gurr's medium. Later I substituted for this rather tedious method the smear method described by Taylor (1924), which permits the use of a greater range of stains. The stain principally used was Gentian Violet. By dehydrating in alcohols containing 1 grm. per cent. each of iodine and potassium iodide, it was possible to obtain stains of any intensity required, while the transparency of the cytoplasm renders easy the examination of thick sections or smears.

A long resting period intervenes between the final archesporial divisions and the beginning of synapsis, so that it is not possible to trace the chromosomes of the preceding anaphase into the meiotic prophase. At the end of the resting period, however, the formation of zigzag threads, very similar to those of the ordinary prophase, precedes the lengthening out into the leptotene threads which are impossible to count, though free ends can occasionally be seen. A certain amount of contraction of the chromatin accompanies the development of the nucleus from this stage to that of fig. 20 (Pl. **9**). This contraction, as Miss Sargant long ago pointed out, can be observed very easily in fresh material, the chromatin being very plainly visible collected towards one side of the nucleus. Great differences occur between the visibility of the chromatin at different stages, when examined as fresh material. Between zygotene and diakinesis I have been unable to see it at all. In the interphase following the first meiotic division it is very plain, but I have not succeeded in observing it later than the anaphase of the second meiotic division.

Though a certain amount of contraction towards one side of the nucleus actually exists, I believe that a tight synaptic knot is never formed in *Tulipa* for I have only seen it in fixed and embedded material, the corresponding anthers examined by smear showing only slight contraction. This stage is of long duration, two to three weeks, and during it there is a gradual arrangement of the leptotene thread into parallel lengths, but no actual conjugation occurs (*cf.* Pl. **9**. figs. 17 & 18). The conjugation, when it takes place, takes place quickly, though occasional pairs may lag behind the rest, as is shown in Pl. 9. fig. 21. Figures 19 and 20 show the process plainly and are typical of the stage in the mixture of thick and thin threads, which caused Janssens to give it the name amphinema. The occurrence of such pairing is not in dispute except in a few definite plants, of which the best authenticated example is *Œnothera*. There is, however, a difference of opinion as to the value of the threads actually uniting. Miss Digby (1919) regards the whole process up to this point as equivalent to the early prophase in a somatic division, so that these pairing threads are half chromosomes longitudinally split in the preceding telophase, which are now reuniting. While I think that the comparison with the somatic prophase at this stage is somewhat forced, it is evident that no disproof of this view is possible on comparison of the number of threads present before and after pairing. Detailed study of the stages that succeed pairing, especially the determination of the method by which the dyad formed in zygonema becomes a tetrad consisting of four chromatids, is necessary in order to decide between the two interpretations in any particular case. In the tulips belonging to the Eriostemones, which I have examined, the stages from zygotene to the appearance of the second split are exceptionally plain. In *T. linifolia*, studied as an example of those species in which all the chromosomes are terminally attached, these stages are more difficult to follow, and in *Fritillaria Meleagris*, in which there is a quite definite second contraction, I have been unable to determine exactly how the second split appears. *Fritillaria* differs much from *Tulipa* and suggests in many ways a comparison with *Stethophyma grossum*, as described by Janssens, a comparison I hope to complete in a later paper.

In fig. 21 (Pl. 9) the pairing is almost completed, but the pairing threads still remain widely separated for a short distance in one segment of the spireme. This figure is taken from a tetraploid species, and it is significant that the pairing is precisely as in the diploid forms. Nevertheless there is in this particular form a tendency for some of the bivalents to associate in pairs at diakinesis.

The completion of pairing is followed by the thickening and shortening of the bivalent threads. Whole flowers may be found in which all the pollen mother-cells are in the zygotene or the succeeding thick spireme stage, which lasts a considerable time. It is followed by the diplotene stage in which the division between the conjugating threads once more becomes evident. Wherever this stage is found, succeeding stages up to metaphase can be found in the same anther, often in the same loculus. The stages by which these double threads develop into the haploid number of bivalent chromosomes can therefore be followed in detail. At first the only difference from zygotene is the slightly increased sharpness of separation between the paired chromosomes. Soon the parallelism between the components of the double thread is broken by the appearance of twistings (*cf.* figs. 22 and 23, Pl. **9**) along a portion of their length. This twisting becomes a more and more conspicuous feature up to diakinesis. There is often a small plasmasome at one end of the double thread (Pl. **9**. fig. 23) to which it seems to be attached. Further shortening accompanied by still sharper separation of the threads permits the haploid number of bivalents to be determined.

Up to this time the individual threads of each pair have shown no sign of doubleness, but this now becomes apparent at first at one end of the bivalent (Pl. **9**. fig. 24 *a* & *b*). The opening of the split rapidly takes effect from one end to the other of what is now the tetrad (Pl. **9**. fig. 25). The tetrad still shows one or more nodes at which the two main branches meet. At some of these nodes there is an apparent change in the plane in which chromatids are separated, with the result that a chromatid at such a node changes the partner with which it is in close association. Two of these nodes may be present at a very early stage, and I have not been able to determine that such a stage is preceded as it is in *Phrynotettix* (Wenrich (1916)) by the complete closing of the reductional split as the equational opens. The tetrads are often much twisted, a feature which becomes still more conspicuous as they continue to shorten, while the fact that longitudinal splits are present is only betrayed by occasional indications, especially at the ends of chromatids (*cf.* Pl. **9**. fig. 26 *b*). Much of the twisting disappears in diakinesis which is characterized by the wide opening of one or other of the planes which divide the tetrad into four chromatids. The four chromatids, however, continue to be closely apposed at one or more points, and the number of these nodes determines the final shape in which the tetrad goes on to the metaphase spindle, whether as a simple rod tetrad, a cross, or a simple or more complex ring. The nodes are of two kinds. In one, the chromatids exchange partners as is described above, in which case the plane in which the chromatids lie rotates through a right angle at the node; in the other, which is most commonly found at the end of the tetrad, the chromatids touch without interlacing. Types of tetrad found in *T. australis* are shown in Pl. **9**. fig. 31 *a* to *l*. In fig. 31 *a* the threads do not touch in the middle of the tetrad, but one passes under the other. In fig. 31 *b* & *l* there is interchange of threads at each of the three nodes, and the tetrad goes on to the spindle in the form of a double ring. No more than two double rings have been observed in any one nucleus of *T. australis*, and quite often there is none. The shorter chromosomes generally form crosses, but examples are figured (Pl. **9**. figs. 28 & 30) where short chromosomes have formed rings. The number of crosses may rise to eight or drop to four.

The arrangement of the tetrads on the spindle depends on the position of the point of attachment, the arms in which the latter lie arranging themselves in a plane at right angles to the equator. In *T. linifolia*, in which the attachment of all chromosomes is terminal, axial rings occur only when there is simple fusion without the formation of transverse lugs at the proximal ends.

In crosses all gradation in relative length of the arms are found, and the arrangement on the spindle depends on the position of the point of attachment. In extreme cases the tetrad may become almost a straight rod, either perpendicular to, or in the plane of, the equator. The former arrangement is possible with sub-median or terminal attachment, the latter only with terminal attachments. Very closely allied to the cross is, however, the equatorial V tetrad, which splits along both arms in the first meiotic division, and at the point of the daughter V in the second division. This form is found in *Tulipa linifolia* and in *Fritillaria.* The only difference from the cross is that the equatorial arms form an angle of less than 180°. The two tetrads in *Fritillaria*, formed from chromosomes with sub-median attachment, are very interesting. They form a cross which consists of pairs of chromatids apposed only at their point of attachment. The plane of division at metaphase passes through all four arms of the cross. It is a point of contrast between *Fritillaria* and *Tulipa*, that whereas in the latter the chromatids interlace or become apposed at several points, in *Fritillaria* there is never more than one point at which all four chromatids touch and this agrees in every instance with the point of attachment. The result is, of course, that no figure more complicated than the cross is formed in *Fritillaria.*

The above description makes it plain that the reduction divisions in *Tulipa* and in *Fritillaria* follow, in general, the parasyndetic scheme worked out by the Schreiners (1906) in *Tomopteris*, while the resemblance to Orthopteran spermatogenesis as described by McClung, Wenrich, and Janssens is remarkably close. Janssens, of course, differs from other authors in his interpretation of the crosses and rings as leading to an actual interchange of material between chromatids, an interpretation which is the only alternative to that proposed by McClung and Granata for the same figures and afterwards elaborated by Robertson and Wenrich. The latter hypothesis, which explains the diakinetic figures as due to the opening out in two planes at right angles of what are originally four parallel chromatids, is adequate to explain the events of diakinesis and division in *Tulipa* and *Fritillaria.* I have made preparations of *Lilium* spp. in order to determine whether the same conditions hold in that genus. The early diakinesis is much less clear in *Lilium*, and though the complex rings divide as they do in *Tulipa* I have not found it possible to recognize the interchange of partners between the four chromatids in diakinesis. A definite proof of the chiasmatypy hypothesis, however, involves the demonstration that this stage does not exist.

In the prophase of the second meiotic division the spiral structure of the chromosomes is very conspicuous. Indications of this structure first appear in telophase I, and may persist up to the passage of the chromosomes into the spindle in metaphase II. The spiral may be so close in prophase that unless staining is very sharp, the individual chromosomes may appear to be already split for the first division in the pollen-grain. Mohr (1914) describes a similar appearance of the chromosomes of *Locusta* at a corresponding stage in the maturation of the germ-cells. He is inclined to connect the appearance of the spiral with the rapidity with which the second division follows the first. In somatic prophases zigzag filaments which may be interpreted as spirals also occur (*cf.* Bonnevie, 1908), though the structure is usually less obvious. In the first meiotic interphase the extreme elongation of the chromatin threads that is characteristic of the somatic interphase is omitted, and the appearance of a network produced by fine and convoluted threads is absent. As a rule it is possible to distinguish the individual chromosomes throughout the meiotic interphase.

*Note added June* 1926.—Since this paper was sent in for publication there has appeared an account * of the maturation divisions in *Allium ursinum*. The author clearly figures the mode of division of the tetrads or, as he prefers to call them, staurosomes. If the author is correct in asserting that the homotypic split does not occur until metaphase I. in *Allium*, the figures given represent a true crossing over effected at metaphase. Nevertheless the origin of just such tetrads (apart from the position of the point of attachment) in *Tulipa* and *Fritillaria* is such that the mode of division described separates chromatids that can already be recognized as distinct entities in prophase. In these cases peculiar shapes of the tetrads may, as Morgan suggests, be the result of a crossing over that has taken place at an earlier stage, but they are certainly not the occasion of a material cross over at metaphase. It is unfortunate that the stages immediately preceding diakinesis are meagrely represented in Chodat's figures.

## SUMMARY.

The basic number of chromosomes in *Tulipa* is twelve and diploid, tetraploid, and hexaploid varieties and species occur. Great differences in size of chromosomes are found among the diploid species. The size of the nucleus is correlated with the size and number of the chromosomes it contains. Correlation of nuclear and somatic size only holds between tetraploid and diploid forms of the same species.

*Tulipa galatica* Fresn. has sixteen chromosomes of which four are very small and unrepresented in the most nearly allied species. The increased number is regarded as being due to transverse fragmentation.

Differences between the species exist in the form of the chromosomes and in their size relative to one another, even where no difference of number is present. Two pairs of chromosomes with sub-median attachment are found in *Lilium*, *Fritillaria*, and in most species of *Tulipa*.

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* R. Chodat: "Le Chiasmatypie et la cinèse de maturation dans l'*Allium ursinum.*" Bull. Soc. Bot. Genève, Août 1925.

The doubtful correctness of the position of *Calochortus* in the Tulipeæ is emphasized by the cytological differences that distinguish it from the other genera. The chromosome numbers found are seven, nine, and ten. Well-marked satellites occur in this genus and in conjunction with differences in size and attachment enable each chromosome in the haploid set to be distinguished individually. *Calochortus Vesta,* a tetraploid series, has four representatives of each of the seven kinds of chromosomes.

In the species (*T. primulina*, *T. australis*, *T. Orphanidea*) especially studied, synapsis involves the lateral pairing in the leptotene stage of threads representing whole chromosomes. Later the split separating the conjugants reappears, and each conjugant becomes longitudinally split giving a tetrad consisting of four chromatids, which become separated in the first and second meiotic divisions.

The forms taken on by the tetrads in diakinesis —rings, crosses, etc.—are regarded as being due to the opening out alternately of the reductional and equational splits. No cytological proof of the existence of crossing over has been found.

This work has been carried out whilst holding a studentship of the John Innes Horticultural Institution, and I have to record my gratitude to the late Dr. Bateson for his unfailing interest and encouragement.

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## EXPLANATION OF THE PLATES.

The drawings were made at the height of the stage by means of an Abbe camera lucida, the objectives used being a 1·5 mm. Zeiss and a 2 mm. Swift aprochromatic oil-immersion lens. Figs. 1–9 were drawn at a magnification of 2700, figs. 10–16 at 3600, the remainder at 2200, except where otherwise stated.

### Plate 7.

Fig. 1. *Tulipa linifolia*. Metaphase plate from root-tip.
2. *T. Batalini*. „ „
3. *T. Kolpakowskiana*. „ „

Fig. 4. *Tulipa primulina.* Metaphase plate from root-tip.
5. *T. Orphanidea.* „ „
6. *T. sylvestris major.* „ „
7. *T. Greigi.* „ „
8. *T. armena.* „ „
9. *T. galatica.* „ „

### PLATE 8.

(All figures × 3600.)

Fig. 10. Anaphase chromosomes from divisions in the root-tip showing the different types of chromosomes which it has been possible to distinguish at this stage.
a. *Tulipa primulina*; b. *T.* "*Murillo*"; c. *T. Greigi*; d. *T. galatica*; e. *T. armena*; f. *T. linifolia*; g. *T. Clusiana*; h. *T. Kolpakowskiana*; k. *T. armena.* Early anaphase in root-tip showing the point of attachment being drawn past the distal end of a daughter chromosome. The attraction is effective only at a definite point.
11. *Calochortus catalinæ.* Late metaphase. Distal trabant in one member only of the pair of chromosomes with median attachments.
12. *C. catalinæ.* Anaphase in same individual. The trabant is much more widely separated from the rest of the chromosome.
13. *C. Vesta.* Each type of chromosome is represented four times.
14. *C. Plummeræ.* Metaphase. Eighteen chromosomes.
15. *C. Benthami.* Metaphase. Twenty chromosomes.
16. *C. amabilis.* Metaphase. Twenty chromosomes.

### PLATE 9.

Fig. 17. *Tulipa Orphanidea.* Leptonema. Early stages in pairing visible in some threads.
18. Leptonema. Parallelisms more numerous.
19. Zygonema. Parallelism of threads complete throughout the nucleus. Conjugation has taken place in a few cases.
20. Zygonema. The thick double threads show where conjugation is completed.
20 *a.* Detail from fig. 20 ×3600.
21. *Tulipa Whittalli.* Tetraploid form. Conjugation almost complete.
22. Diplonema. Note parallel course followed by many twistings. × 3600.
23. Diplonema. Later stage. Four of the twelve bivalents only are drawn. Some threads appear to be attached to small plasmosomes.
24 *a.* Slightly later stage. Each conjugant shows doubleness.
*b.* Each conjugant split throughout.
25. Eleven bivalents from early strepsitene nucleus, the twelfth was nearly perpendicular to the plane of the paper and could not be drawn.
26. Further condensation accompanied by twisting obscures partly or entirely the double nature of each member of the bivalent.
27. Diakinensis. Smear. × 1700. *T. Orphanidea.*
28. *T. Orphanidea.* Diakinesis.
29. *T. australis.* Late diakinesis.
30. *T. Orphanidea.* Smear. Nine crosses, no double ring.
31. *T. australis.* The twelve bivalents of a single nucleus in early diakinesis. The interrelations of the four chromatids are plain, but later it becomes very difficult to distinguish between simple twisting and interchange of partners by the chromatids.

## PLATE 10.

Fig. 32. *Tulipa Orphanidea.* Individual tetrads showing interchange of partners.

33. *T. Clusiana.* Metaphase. Twenty-four bivalents, twelve univalents.

34. *T. linifolia.* Metaphase. The individual chromosomes are equal in size to those of *Clusiana.* The range in form of the bivalents is not affected by the difference of attachment as compared with *australis.*

35. *T. Orphanidea.* Early anaphase. Equatorial and tangential rings.

36. *T. linifolia.* Tangential and double rings.

37. *T. Orphanidea.* Later anaphase. Single and double Vs.

38. *T. linifolia.* Anaphase. Single Vs only which separate into rods at the suceeding division. Attachment terminal in all cases.

39. *Fritillaria Meleagris.* Metaphase. The form of the bivalent is determined by the attachment.

40. Beginning of anaphase in *Fritillaria Meleagris.* *a.* is a tetrad with sub-terminal, *b.* one with terminal, attachment; *c.* is the large cross tetrad derived from the chromosomes with sub-median attachment; *d.* is a rod tetrad flexed at the point of attachment where separation is effected; *e.* is a V tetrad with very widely separated arms viewed on face.

41. Later stage in anaphase. The method by which the anaphase double Vs are produced by tetrad *b* is shown.

42. *Lilium candidum.* Metaphase showing peculiar E chromosome and the fact that the apparently twisted chromosomes divide as if they were complex rings.

43. Late diakinesis. *Fritillaria Meleagris.*

44. Spiral structure in prophase II. *Fritillaria Meleagris.*

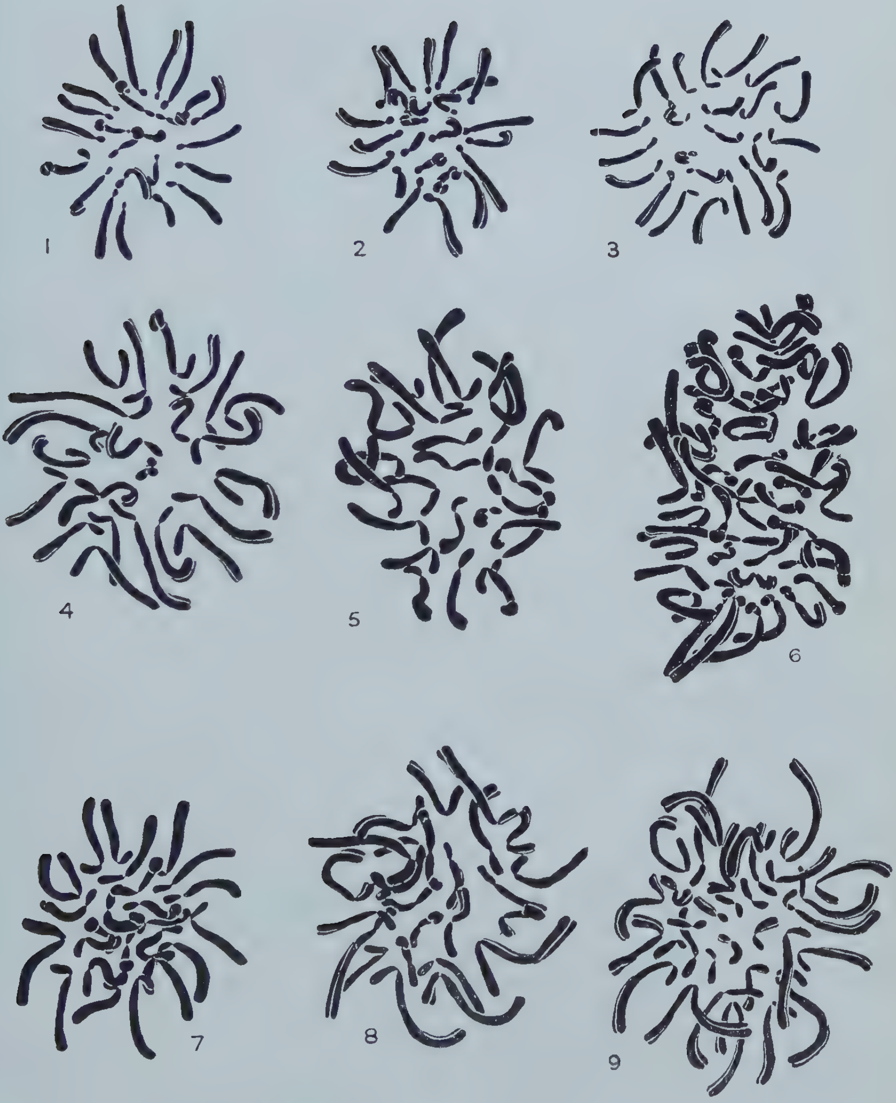
*a.* Chromosomes on spindle of metaphase II. in *Fritillaria Meleagris* still showing traces of spiral structure.

45. *Tulipa humilis.* Successive sections of embryo-sac with anaphases of second division. The vacuole is at the chalazal end. × 960.

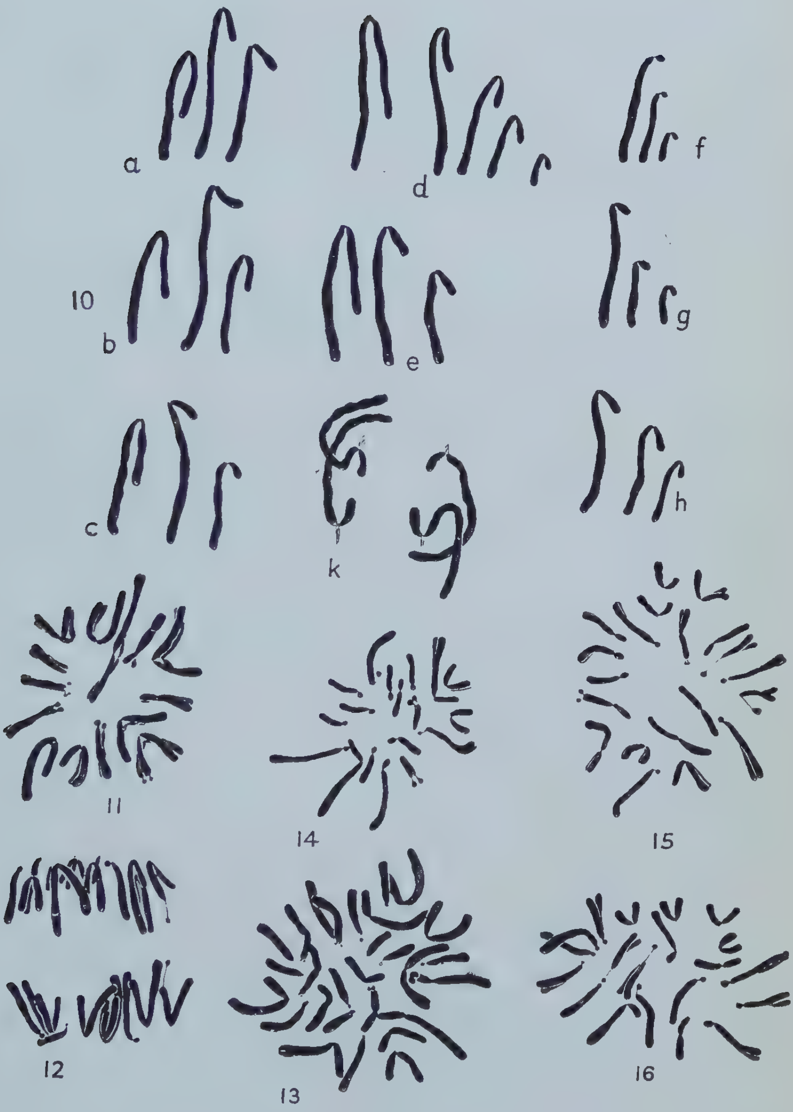
46. *T. Kolpakowskiana.* Metaphases of second divisions. The micropylar plate has 12 chromosomes, the chalazal 24 or 25. × 1700.

47. Same species. Arrangement of nuclei in four-nucleate sac. × 450.

48. Same species. Failure of division in the micropylar nucleus. × 450.



CHROMOSOMES OF TULIPA.



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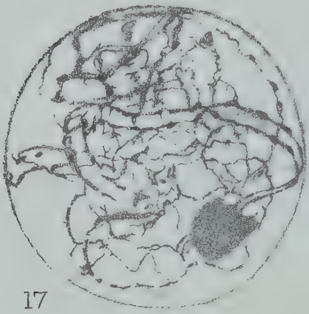
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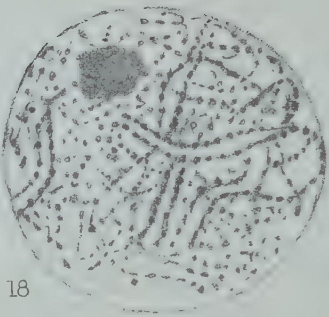
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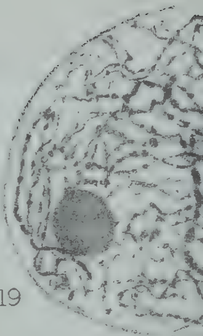
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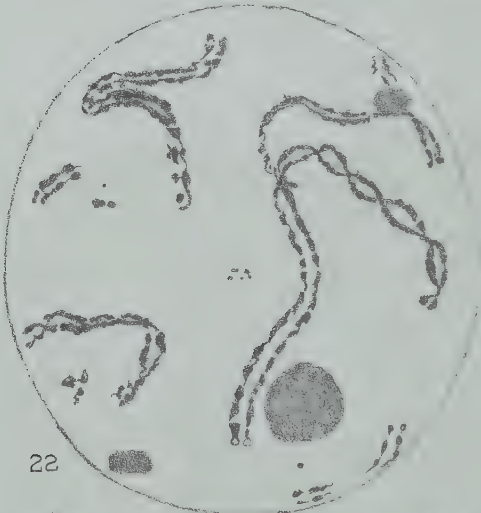
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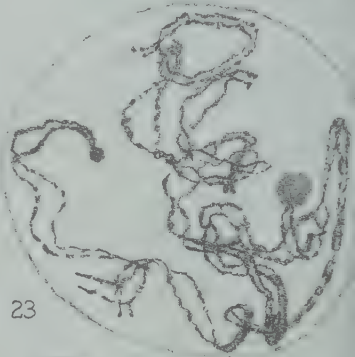
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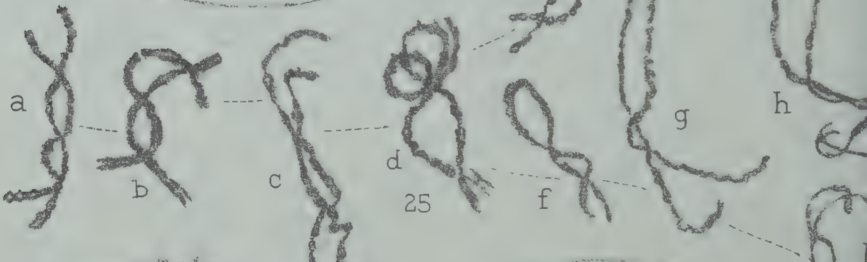
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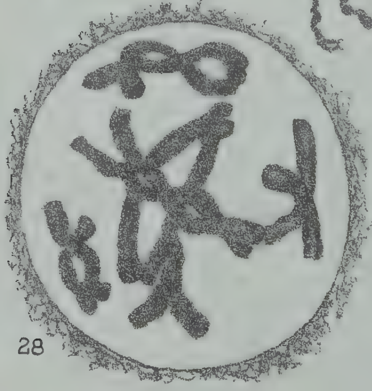
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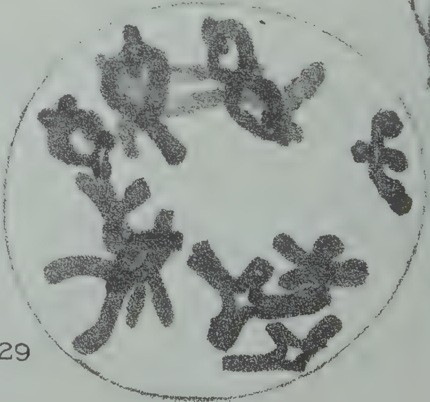
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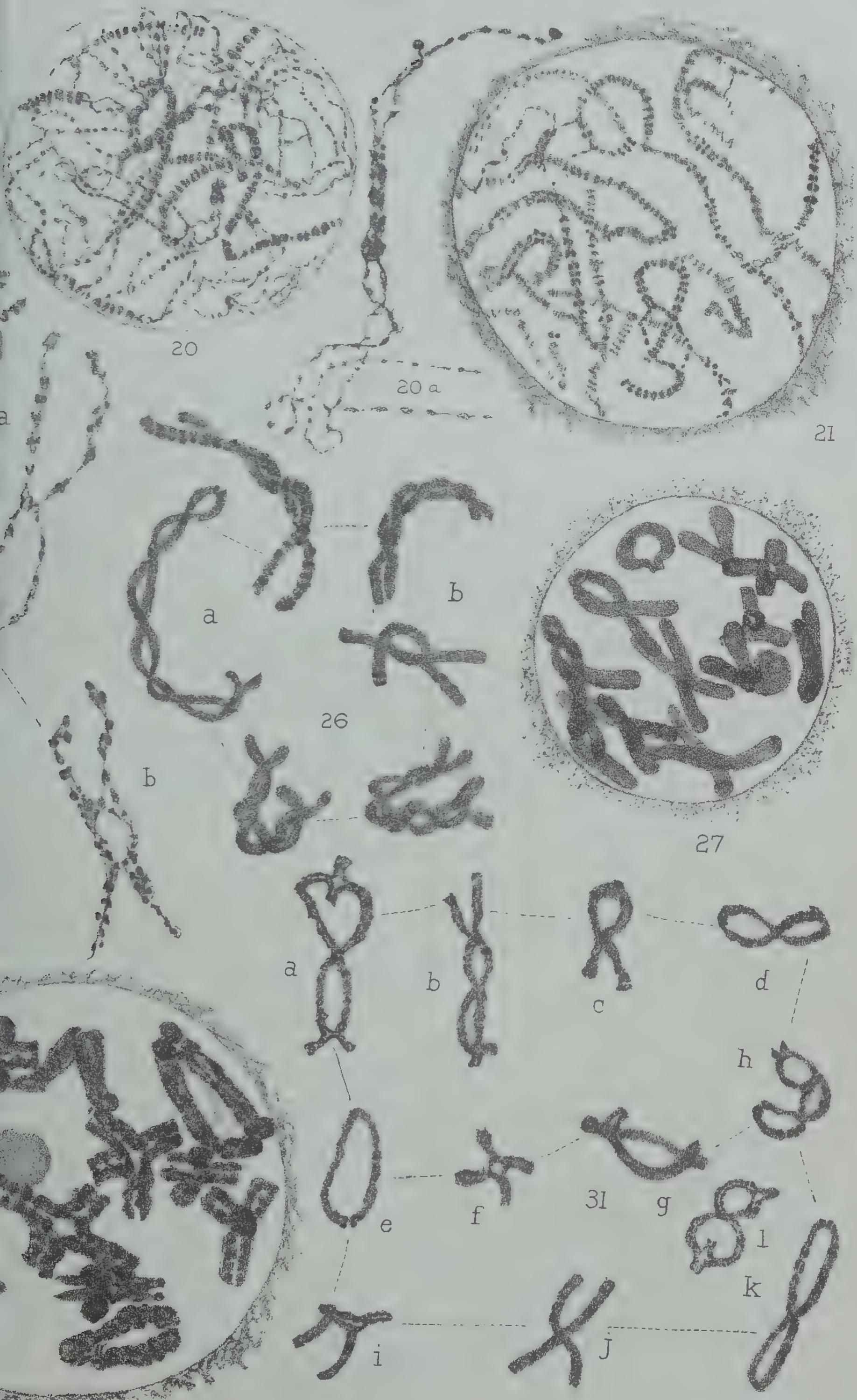
W. C. F. N. del.
P. Highley Lith.

CHROMOSOMES



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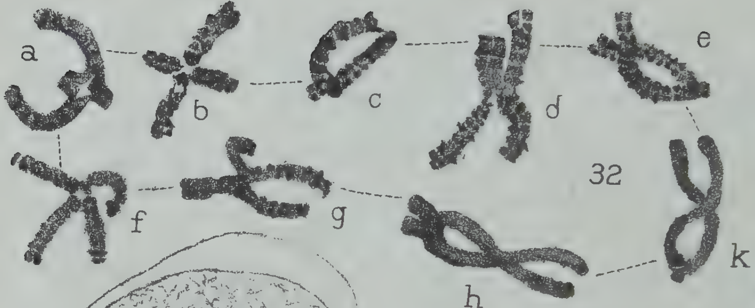
OF TULIPA



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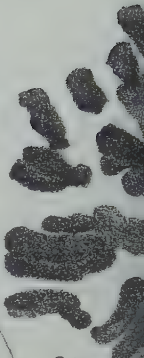

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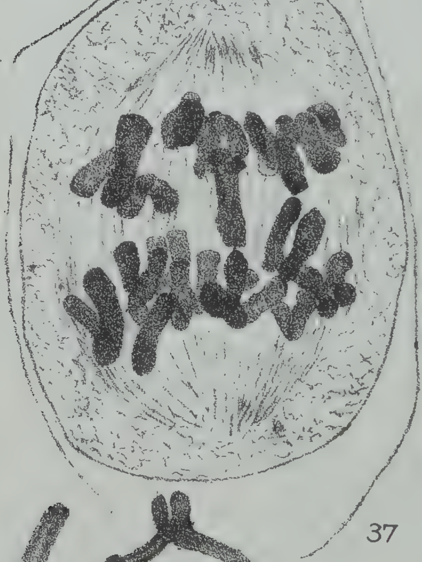

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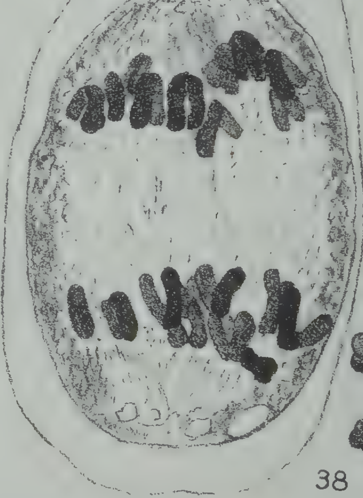

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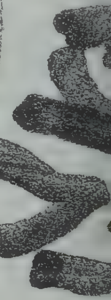

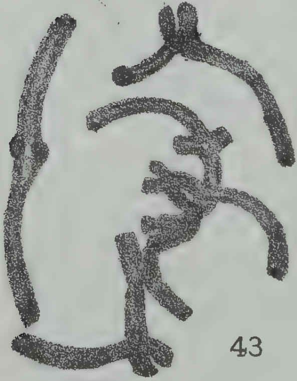

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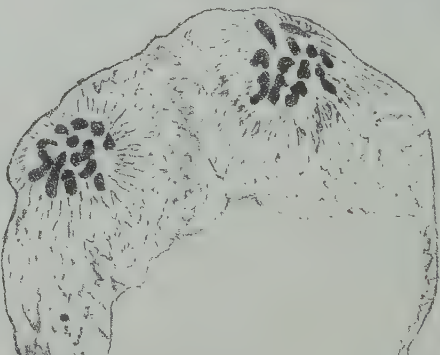

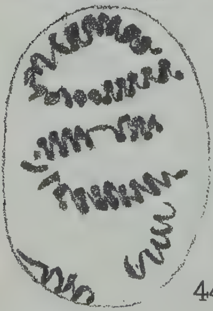

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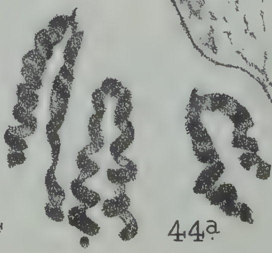

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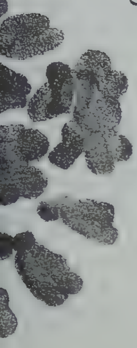
P. Highley. Lith.

CHROMOSOMES



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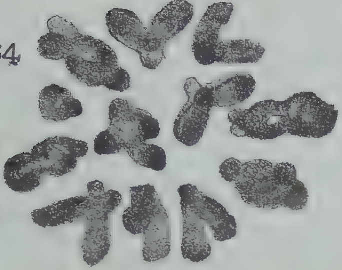

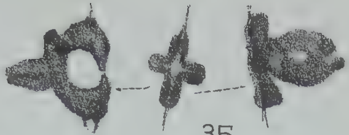

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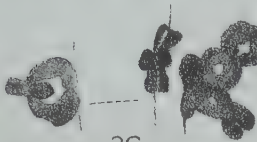

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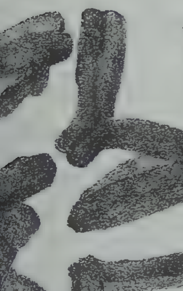

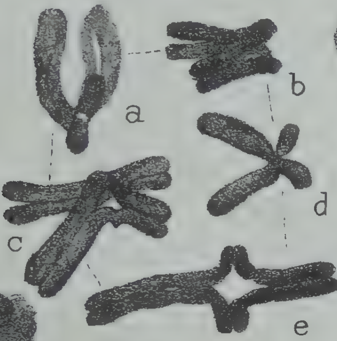

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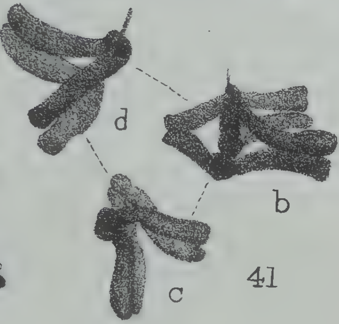

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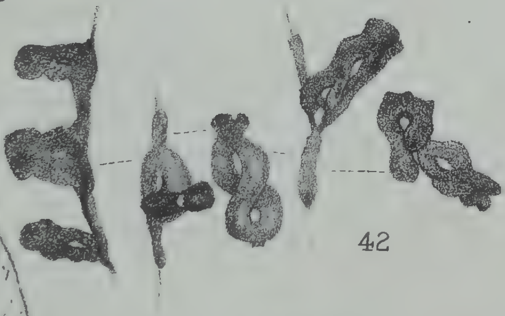

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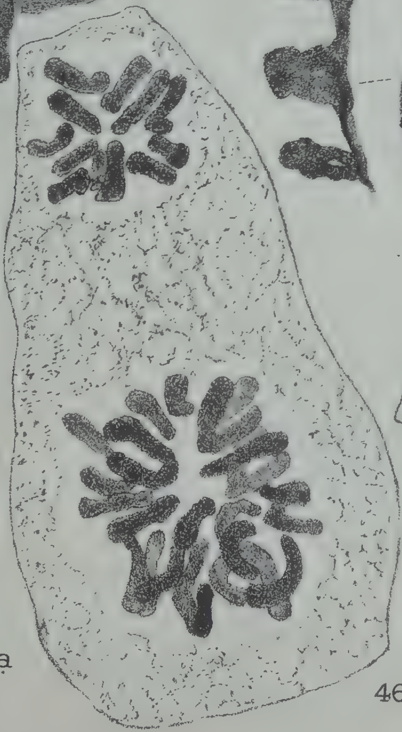

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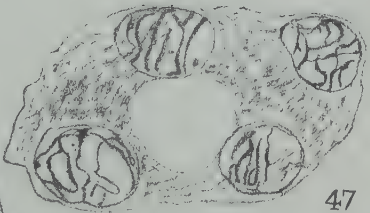

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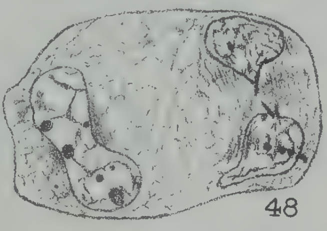

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# Studies in the Phytoplankton of the Lowland Waters of Great Britain. No. IV. The Phytoplankton of the Isle of Anglesey and of Llyn Ogwen, North Wales. By BENJAMIN MILLARD GRIFFITHS, D.Sc., F.L.S.

[Read 6th May, 1926.]

## INTRODUCTION.

THE Island of Anglesey lies off the coast of North Wales, immediately to the north of the great Snowdonian massif, and separated from the latter only by the very narrow and riverlike Menai Strait. In geographic character, Anglesey is entirely different from the mountainous country on which it abuts. The island is a plain, which for the most part does not rise more than three hundred feet above sea-level. The land, too, is fertile and well cultivated, mostly as pasture. There are very few woods and these are of small extent. Bogs and heaths are infrequent, the latter occurring on the seaward side where there are fairly wide stretches of sandy ground, probably of wind-blown origin. Geologically, Anglesey is composed of some of the most ancient rock in the British Isles, the north-western two-thirds being of pre-Cambrian age, but the south-eastern third is of Carboniferous strata (Greenly, **2**).

On the north-western area of ancient rock there lie some half-dozen small lakes or lynns, of which the majority have rocky sides and floors, and a water-supply derived from ancient rock. In August 1923, the writer examined the plankton of five of these, viz.: Traphwlls, Penrhyn, Coron, and Maelog, all of which lie not far from the sea on the western side, and the lake at Presaddfed which lies further inland. The collections were taken with the usual conical silk net of ·05 mm. mesh, and the catches were immediately preserved with 2 per cent. formic aldehyde solution The hydrogen ion concentration of the water was taken with a "universal indicator" giving a range from 4·0 to 11·0, the test being made on the spot in each case.

In addition to the Anglesey Lakes, the writer also examined the plankton of Llyn Ogwen, a lake of about the same size and contour as the former, but situated at a height of about a thousand feet among the Snowdonian mountains, and lying under the steep and craggy slopes of the Nantfrancon Pass on the way to Capel Curig. Speaking of the Welsh lake-area, Messrs. West state :—"The desmid flora in certain of these lakes is equal to that found in the richest lakes of the north-west of Scotland, and in one case—the Capel Curig Lakes—is superior to that known from any other lake in the world which has been biologically investigated" (West & West, **14**, p. 173). At the time of the visit, the weather was so exceedingly stormy that no boat was allowed out on the lake, and the collection was made from the side, at a point where the bare rock of the basin dipped steeply into deep water.

The pioneer work of Messrs. W. and G. S. West on the British freshwater phytoplankton was carried out for the most part on the lakes of the Scottish Highlands, the Cumbrian Lakes, and the Welsh Lakes, all of which are situated on ancient rock but in areas which are mountainous in character. The Anglesey lake-area offers an interesting contrast, in that although the area is one of very ancient rock, it is nevertheless not mountainous in character, but approaches very closely in type to that of the country found in the broad stretches of newer rocks which extend in a great plain from the Welsh Mountains eastward to the Urals in Russia. The Anglesey area is paralleled both topographically and geologically by certain districts in southern Sweden, whose numerous and varied waters have been investigated by Naumann and his co-workers.

## THE TOPOGRAPHY AND PHYTOPLANKTON OF THE ANGLESEY LAKES.

### Llyn Traphwlls (pron. Trafoothlse or Treffles).

Area about 80 acres; depth from five to twenty feet. The lake is completely natural. It lies in a basin of solid rock of pre-Cambrian age, and is situated amidst rough rocky pasture, out of which protrude large masses of the underlying strata. On the north-east side is a little arable land. In places the shore drops straight into deep water. The bottom is said to be gravelly. The water is carefully protected from contamination because the lake is used as a reservoir. The inflowing streams are small and slow.

In the shallower bays are small masses of *Scirpus lacustris*, together with a good deal of *Sparganium*, *Polygonum amphibium*, and occasional *Nuphar*.

The plankton was abundant, giving the water a granular appearance. The pH of the water as determined colorimetrically, was 8.

The contents comprised:—Dominant: *Ceratium hirundinella*, with two normal basal horns and one smaller one; *Asterionella formosa* with eight rays; *Melosira granulata*. Abundant: *Microcystis æruginosa*, *Anabæna affinis* var. *intermedia*, *Pediastrum duplex*, *Microcystis scripta*. Many: *Gomphosphæria Naegeliana*, *G. lacustris*, *Anabæna Lemmermanni*, *Fragilaria Crotonensis*, *Closterium aciculare* var. *subpronum*. Rare: *Staurastrum gracile*, *S. paradoxum*, *S. paradoxum* var. *biradiatum*, *Dictyosphærium pulchellum*, *Botryococcus Braunii*.

### Llyn Penrhyn.

This lake is situated close to Traphwlls and is of similar size and about the same depth. On the west is rough rocky pasture, on the north-east is a little marshy ground with arable and pasture behind, and on the south is heathy pasture. Three sides of the basin are solid rock, but the south side is composed of sandy ground, on which is the dry heath stretching away seawards. On the west side is a long narrow fringe of *Scirpus* mixed with a little *Arundo* and much *Nuphar*. The water was clear but granular. The pH was indicated as 8. The plankton was abundant and comprised :—

Dominant : *Rivularia echinulata*, *Asterionella formosa*, eight rayed. Many: *Anabæna Lemmermanni*, *Volvox globator* (some with oospores), *Anabæna* sp. (straight and slender but without spores), *A. affinis* var. *intermedia*. Few : *Staurastrum paradoxum*, *S. paradoxum* var. *biradiatum*, *Microcystis Flos-aquæ*, *Eudorina elegans*, *Dictyosphærium pulchellum*, *Ceratium hirundinella* with two basal horns, *Dinobryon Sertularia*.

### Llyn Coron.

This lake is about the same size as Penrhyn but rather less deep. Three sides and the floor are rocky, but on the west the shore consists of a steep bank of sand which is the edge of a sandy heath stretching away to the sea. The bottom is weedy at the edges. Fringing vegetation is very scanty and consists of one or two small masses of *Scirpus* on the north side and a small fringe of *Polygonum amphibium* on the sandy west shore. The lake is surrounded by pasture. A strong stream enters on the east and flows out at the north-west angle. There was a grey-green water-bloom. The abundant plankton comprised :—

Dominant : *Rivularia echinulata*, *Anabæna affinis* var. *intermedia*, *A. Lemmermanni*, sporing very freely, *Pediastrum duplex*. Many : *Microcystis Flos-aquæ*, *Asterionella formosa* with eight rays. Rare : *Staurastrum paradoxum* var. *biradiatum*, *Microcystis firma*, *Dictyosphærium pulchellum*.

The pH of the water was indicated as 8.

### Llyn Maelog.

The area of this lake is the same as that of the last, but the depth is said to be only some seven feet. The bottom is said to be muddy. The three landward sides are of solid rock, but the seaward side consists of a rather narrow line of fixed sand-dunes which are marshy towards the lake. The lake is so close to the sea that on occasion sea-water comes in. The seaward edge is fringed with a broad belt of *Arundo* with a little *Scirpus*. The water was clear but granular. The plankton was abundant and comprised :—

Dominant : *Rivularia echinulata*. Many : *Ceratium hirundinella* with three basal horns, but rather small in size. Few : *Microcystis æruginosa*, *Botryococcus Braunii*.

Presaddfed Lake.

This lake is situated some miles from the sea, and is entirely surrounded by arable and pasture. Although the area is nominally 170 acres, about three-quarters of it is silted up and covered with *Typha angustifolia* and smaller patches of *Polygonum amphibium.* The depth is scarcely over six feet. The bottom varies in condition from muddy to gravelly, but in many places the sides are of solid rock. The lake is slightly raised in level by a low dam, and the height of the water varies from season to season. The low slope of the sides and the consequent shallowness of the water at the edge, encourages the growth of submerged aquatics, and the area of open water is therefore of relatively small extent. The water was clear and the plankton was not abundant. The pH was indicated as 8.

Two collections of plankton were taken, one from the open water free from weeds, and the other from water containing weeds among whose submerged fronds the plankton net was drawn. The contents were as follows :—

From the open water :

In fair numbers: *Xanthidium antilopæum*, *Botryococcus Braunii*, (*Hyalotheca mucosa*), *Eudorina elegans*. In very small numbers : *Staurastrum avicula*, *S. gracile*, *Spondylosium papillosum*, *Sphærozosma vertebratum*, *Arthrodesmus convergens*, *Dictyosphærium pulchellum*, (*D. Ehrenbergianum*, *Staurastrum lunatum* var. *planctonicum*, *S. erasum*, *Asterionella formosa* with eight rays, *Ceratium hirundinella*, *Merismopedia glauca*, *Cœlastrum sphæricum*, *Kirchneriella obesa*, *Staurastrum furcigerum*).

From the weedy water :

Those above which are not enclosed in brackets, together with the following species, none of which were plentiful :—*Cosmarium Meneghinii*, *C. impressulum*, *C. granatum*, *C. fontigenum*, *C. punctulatum*, *Staurastrum dejectum*, *S. gracile* var. *nanum*, *S. Manfeldtii*, *S. Bieneanum* var. *ellipticum*, *Closterium Venus*, *Arthrodesmus Incus* var. *Ralfsii* forma *latiuscula*, *A. octocornis*, *Micrasterias Crux-Melitensis*, *Euastrum dubium*, *Hyalotheca dissiliens*, *Sphærozosma Wallichii* var. *anglicum*, *Pandorina Morum*, *Ankistrodesmus falcatus.*

*Phytoplankton of Anglesey Lakes*, 1923.

| ccc=abundant; cc=common; c=fairly common; r=few; rr=rare; rrr=very rare. | Traphwlls. 1 | Penrhyn. 2 | Coron. 3 | Maelog. 4 | Presaddfed. (Open water.) 5 A | Presaddfed. (Weedy water.) 5 B |
|---|---|---|---|---|---|---|
| BACILLARIEÆ. | | | | | | |
| *Melosira granulata* (Ehrenb.) Ralfs | ccc | | | | | |
| *Fragilaria Crotonensis* (A. M. Edw.) Kitton | c | | | | | |
| *Asterionella formosa* Hass. | ccc | ccc | c | .. | rrr | |
| MYXOPHYCEÆ. | | | | | | |
| *Anabæna affinis* var. *intermedia* Griff. | cc | c | ccc | | | |
| ,, *Lemmermanni* P. Richter | c | c | ccc | | | |
| ,, sp. | .. | c | | | | |
| *Merismopedia glauca* (Ehrenb.) Naeg. | .. | .. | .. | .. | rrr | |
| *Gomphosphæria Naegeliana* (Unger) Lemm. | c | | | | | |
| ,, *lacustris* Chodat | c | | | | | |
| *Microcystis æruginosa* Kuetz. | cc | .. | .. | r | | |
| ,, *Flos-aquæ* (Wittr.) Kirchn. | .. | r | c | | | |
| ,, *scripta* (Richter) Lemm. | c | | | | | |
| ,, *firma* (Bréb. et Lenorm.) Rabenh. | .. | .. | r | | | |
| *Rivularia echinulata* J. E. Smith | rrr | ccc | ccc | ccc | | |
| PROTOCOCCALES. | | | | | | |
| *Volvox globator* Ehrenb. | .. | c | | | | |
| *Eudorina elegans* Ehrenb. | .. | .. | .. | .. | c | c |
| *Pandorina Morum* (Muell.) Bory | .. | .. | .. | .. | .. | r |
| *Pediastrum duplex* Meyen | cc | . | cc | | | |
| *Cœlastrum sphæricum* Naeg. | .. | .. | .. | .. | r | |
| *Ankistrodesmus falcatus* (Corda) Ralfs | .. | .. | .. | .. | .. | r |
| *Kirchneriella obesa* W. & G. S. West | .. | .. | .. | .. | rrr | |
| *Dictyosphærium pulchellum* Wood | r | r | .. | .. | r | r |
| ,, *Ehrenbergianum* Naeg. | .. | .. | .. | .. | r | |
| *Botryococcus Braunii* Kuetz. | rrr | .. | .. | r | c | c |
| *Ceratium hirundinella* O. F. M. | ccc | r | .. | c | rrr | |
| *Dinobryon Sertularia* Ehrenb. | .. | r | | | | |
| DESMIDIEÆ. | | | | | | |
| *Closterium aciculare* var. *subpronum* W. & G. S. West | c | | | | | |
| *Staurastrum gracile* Ralfs | r | .. | .. | .. | r | r |
| ,, *paradoxum* Meyen | r | r | | | | |
| ,, ,, var. *biradiatum* Griff. | rr | r | r | | | |
| Confined to Presaddfed Lake:— | | | | | | |
| *Closterium Venus* Kuetz. | .. | .. | .. | .. | .. | r |
| *Euastrum dubium* Naeg. | .. | .. | .. | .. | .. | r |
| *Micrasterias Crux-melitensis* (Ehrenb.) Hass. | .. | .. | .. | .. | .. | r |
| *Cosmarium granatum* Bréb. | .. | .. | .. | .. | .. | r |
| ,, *fontigenum* Nordst. | .. | .. | .. | .. | .. | r |

*Phytoplankton of Anglesey Lakes*, 1923 (*cont.*).

| | Traphwlls. 1 | Penrhyn. 2 | Coron. 3 | Maelog. 4 | Presaddfed. (Open water.) 5 A | Presaddfed. (Weedy water.) 5 B |
|---|---|---|---|---|---|---|
| DESMIDIEÆ (*cont.*). | | | | | | |
| *Cosmarium impressulum* Elfv. | .. | .. | .. | .. | .. | r |
| „ *Meneghinii* Bréb. | .. | .. | .. | .. | .. | r |
| „ *punctulatum* Bréb. | .. | .. | .. | .. | .. | r |
| *Xanthidium antilopæum* (Bréb.) Kuetz. | .. | .. | .. | .. | c | c |
| *Arthrodesmus convergens* Ehrenb. | .. | .. | .. | .. | r | r |
| „ *Incus*, var. *Ralfsii* forma *latiuscula* W. & G. S. West. | .. | .. | .. | .. | .. | r |
| „ *octocornis* Ehrenb. | .. | .. | .. | .. | .. | r |
| *Staurastrum Avicula* Bréb. | .. | .. | .. | .. | r | r |
| „ *Bienianum* Rabenh. var. *ellipticum* Wille | .. | .. | .. | .. | .. | r |
| „ *dejectum* Bréb. | .. | .. | .. | .. | .. | r |
| „ *erasum* Bréb. | .. | .. | .. | .. | r | |
| „ *furcigerum* Bréb. | .. | .. | .. | .. | rrr | |
| „ *gracile* var. *nanum* Wille | .. | . | .. | .. | .. | r |
| „ *lunatum* var. *planctonicum* W. & G. S. West. | .. | .. | .. | .. | r | |
| „ *Manfeldtii* Delp. | .. | .. | .. | .. | | r |
| *Spondylosium papillosum* W. & G. S. West | .. | .. | .. | .. | r | r |
| *Sphærozosma vertebratum* Ralfs | .. | .. | .. | .. | r | r |
| „ *Wallichii* var. *anglicum* W. & G. S. West | .. | .. | .. | .. | .. | r |
| *Hyalotheca dissiliens* (Sm.) Bréb. | .. | .. | .. | .. | .. | r |
| „ *mucosa* Ehrenb. | .. | .. | .. | .. | c | |

| Nos. of species :— | Bacill. | Myxo. | Protococ. | Desmid. | Perid. | Dinobryon. | |
|---|---|---|---|---|---|---|---|
| Traphwlls | 3 | 7 | 3 | 4 | 1 | 0 | 18 |
| Penrhyn | 1 | 5 | 2 | 2 | 1 | 1 | 12 |
| Coron | 1 | 5 | 1 | 1 | 0 | 0 | 8 |
| Maelog | 0 | 2 | 1 | 0 | 1 | 0 | 4 |
| Presaddfed (open) | 1 | 1 | 6 | 10 | 1 | 0 | 19 |
| Presaddfed (weedy) | 0 | 0 | 5 | 22 | 0 | 0 | 27 |
| | 3 | 11 | 10 | 29 | 1 | 1 | 55 |
| Shrop. & Cheshire area. | 8 | 13 | 31 | 18 | 7 | 4 | 81 |
| Common to both areas. | 3 | 6 | 9 | 8 | 1 | 1 | 28 |
| Confined to Anglesey | 0 | 5 | 1 | 21 | 0 | 0 | 27 |

Phytoplankton of Llyn Ogwen :—

*Euastrum verrucosum* var. *coarctatum* Delp.
*Micrasterias truncata* (Corda) Bréb.
,, *rotata* (Grev.) Ralfs
*Cosmarium pseudoconnatum* Nordst.
*Xanthidium antilopæum* (Bréb.) Kuetz.
,, *armatum* (Bréb.) Rabenh.
*Staurastrum aculeatum* (Ehrenb.) Menegh.
,, *anatinum* Cook & Wills.
,, *aristiferum* Ralfs
,, *cumbricum* var. *cambricum* West
,, *furcigerum* var. *armigera* Bréb.
*Staurastrum gracile* Ralfs
,, *longispinum* (Bail.) Archer
,, *Ophiura* Lund
*Desmidium aptogonum* Bréb.
*Gymnozyga moniliformis* Ehrenb.
*Hyalotheca dissiliens* (Sm.) Bréb.
*Peridinium Willei* Huitf.-Kaas
*Dinobryon divergens* (Imhof) Lemm.
*Pediastrum duplex* Meyen
*Eudorina elegans* Ehrenb.

The pH was 6·5.

## THE ALGA-FLORA.

The alga-flora does not present any very striking features as such, but nevertheless it is of considerable interest in reference to the relationship of the "desmid" type of plankton to the lowland type exhibited in the waters of Shropshire, Cheshire and elsewhere on the great European plain, both in this country and on the Continent.

The Anglesey lakes mentioned above are situated on one of the most ancient geological areas in Britain, and their basins are in the solid rock. They might therefore be expected to show something in the nature of "desmid planktons." A glance at the list of their contents shows that this is not in the least the case. The Lakes Trapwhlls, Penrhyn, Maelog, and Coron contain but four species of desmids altogether, viz., *Closterium aciculare* var. *subpronum*, *Staurastrum gracile*, *S. paradoxum*, *S. paradoxum* var. *biradiatum*. With the exception of the first species, none of them occur in any quantity, and only the last two are found in more than one pool. None of the desmids are (P) or (Pv) species of Messrs. West (West & West, **14**, p. 177), and only one, *Closterium aciculare* var. *subpronum*, is even a (p) species. All four are found, however, in some of the larger and deeper Shropshire and Cheshire waters :—*Closterium aciculare* var. *subpronum* ; Rostherne, White Sitch. *Staurastum gracile* ; Newton Mere. *S. paradoxum* ; Mere, Knutsford, Combermere, Rostherne, Colemere, White Mere. *S. paradoxum* var. *biradiatum* ; Ellesmere, Newton Mere, Black Mere, Mere, Knutsford, Rostherne, Colemere, White Mere, Patshull Pool, Oss Mere, Isle Pool (Griffiths, **4**). The *Closterium* species also occurs in the Bulmershe South Pool, Berks (Griffiths, **3**).

The Anglesey lakes are so far from being "desmid" in type that they show an alga-flora in which Myxophyceæ, the diatom *Asterionella*, and the Peridinian, *Ceratium hirundinella*, are dominant to a degree sufficient to cause conspicuous water-blooms, just as in the larger and deeper Shropshire and Cheshire lakes. Of the two characteristic Myxophyceæ of the Anglesey lakes, *Anabæna affinis* var. *intermedia* occurs in eight of the Shropshire and southern Cheshire waters (Griffiths **4**, p. 78), and *Rivularia echinulata* was recorded by Phillips as occurring in Ellesmere Lake in great abundance in 1884. The writer did not find it in that lake in 1922, but in the neighbouring lake of Whitemere (Griffiths, *l. c.*). The alga is historically interesting because it is recorded as "sent by the Rev. Mr. Davies from a lake in Anglesey" in 'English Botany' (J. E. Smith and J. Sowerby, vol. xx. *Conferva echinulata*, 1378 ; London, MDCCCV).

It is clear, therefore, that in spite of the antiquity of their rock basins, these Anglesey lakes have planktons which differ entirely from the desmid type of similar areas of rock. Their planktons in fact are not only similar in general character to those of lakes lying on the newer rock areas, but there is actual identity of species in very many instances, particularly the conspicuous and dominant members of the flora. The reason for this is apparent if one takes into consideration the fact that the lake, considered as an ecological habitat, depends not on the one factor of initial water supply, but on the equally important factors of basin contour and of topography (Griffiths, **5**). In the Anglesey lakes, although the area is of ancient rock and is therefore likely to yield a water-supply which is poor in dissolved salts and organic matter, the topography of the drainage area is of a lowland and not of a mountainous character. The low elevation and small gradients permit the formation of a top-soil *in situ*, upon which vegetation can grow undisturbed. The plants absorb salts from the disintegrating rock, and accumulate them in their tissues. As new generations of plants grow faster than the former generations decay, there is a gradual formation of humus, through which the rain must percolate. The water which comes through the humus-mantle and drains into the lake basin, tends therefore to be richer in dissolved matter than if it had merely drained off bare rock. Provided the drainage is fairly good,—and the moderate gradients will ensure this,—the drainage water will tend to be alkaline rather than acidic in reaction. It has already been mentioned that the water of the lakes was uniformly on the alkaline side, and the following official analysis of the water of Llyn Traphwlls shows that the amount of dissolved matter in it is by no means small :—

| Solids. | Chl. | NH free. | NH comb. | Total hard. | Temp. hard. |
|---|---|---|---|---|---|
| 10·4 | 4·7 | ·0024 | ·0168 | 8·0 | 5·5 |

in parts per hundred thousand.

The enrichment of the water is favoured not only by the topography of the drainage area but also by the size of the lake basins. The basins though rocky and fairly steepsided are not very large, and consequently though there cannot be very great developments of fringing vegetation, what there is bears a fair proportion in relation to the volume of the water in the basin, and to that extent assists in enriching the water still further. If the basins had precisely the same curvature but were of much greater absolute size, then the effect of the weed-fringe would be proportionately less. Vegetation, both aquatic and terrestrial, is also favoured by the milder temperatures which occur in this lowland habitat as compared with the more severe climate of mountainous regions.

The great importance of the topographic factor in the habitat factor-complex of the pool, is seen when one compares the foregoing Anglesey lakes with a lake such as Llyn Ogwen. The latter is of fairly similar size and lies on rock of great geological age. As we have seen, the plankton is definitely desmid in type, and Bacillarieæ, Myxophyceæ, and Protococcales are either absent or very rare. The plankton differs almost totally from those of the Anglesey lakes, in spite of the habitat-similarities of size, depth, and antiquity of rock. The cause of the difference lies in the topographic factor, because on these steep and craggy slopes there is a tendency for the disintegrated rock to be swept downwards into the lake, and the formation of a soil in which plants can grow and form humus is hindered. Even if it did form, the much heavier rainfall tends to make the soil waterlogged, and the water, draining imperfectly from boggy pockets, is inclined to be peaty and on the neutral or acidic side. A further topographic difference is the greater severity of the climate due to the elevation and mountainous nature of the area. The lower spring temperature is unfavourable to the growth of macrophytes, and this, combined with the poor quality of the water, and the non-organic type of sediments, checks the growth of weed-fringe and further hinders the enrichment of the water of the lake.

It has been shown by Pearsall that in the Cumbrian Lakes, desmid planktons are associated with neutrality or slight acidity of the water, and poverty in certain dissolved salts and organic matter (Pearsall, **8**, **9**). It is clear that the ecological conditions necessary for this state of affairs are likely to be possible only on areas of ancient rocks, because newer rocks tend to be more calcareous and the water draining from them must be richer in dissolved salts from the beginning. In the ancient rock-area, conditions will only be satisfied provided that the initial water-supply is not enriched in the manner pointed out previously, and that the size and contour of the basin either prevent the occurrence of a weed-fringe, or make the effect of the weed-fringe negligible.

A point of interest in connection with the four Anglesey lakes, is that the number of species in each varies inversely with the distance of the lake from the sea. Maelog, with its four species, is said to receive sea-water occasionally, and the others probably receive sea-spray during strong westerly gales. The rather high chlorine content of Traphwlls may possibly be explained in this way.

Presaddfed Lake has a plankton very different from the other four lakes, and its ecology is very different also. The lake is shallow and very much silted; there is a great quantity of sub-aerial vegetation and no small amount of submerged. The planktonic characters of the desmids, collected in open and weedy water respectively, are shown in the following table:—

| | P. | Pv. | p. | "Littoral." | |
|---|---|---|---|---|---|
| Open Water .................. | | 1 | 3 | 7 .... | 11 |
| Weedy Water.................. | | .. | 1 | 21 .... | 22 |
| Common to both............ | | .. | 1 | 6 .... | 7 |
| Confined to Open ......... | | 1 | 2 | 1 .... | 4 |
| Confined to Weedy ........ | | .. | .. | 15 .... | 15 |

It is strikingly clear from the above table, that even in a small and weedy pool, some species of desmids multiply freely in the neighbourhood of the submerged vegetation, while others find a more suitable habitat in the more open water away from the variations in water-composition which masses of weeds must necessarily bring about during their metabolic activities. (Compare Tabley Pool, Griffiths, **4**, p. 95.) The desmid flora is very different from that of Llyn Ogwen, only *Xanthidium antilopæum*, *Staurastrum gracile*, and *Hyalotheca dissiliens* being common to both. The pH of the water, the basin contour, and the topography are all different also. The desmid flora of Ogwen is the flora of neutral or slightly acidic water, poor in salts and organic matter, and that of Presaddfed is the reverse. Both are on ancient rock, but the basin contour factor and the topographic factor shift the habitat over towards that of lowland pools like the White Sitch (Griffiths, **4**, p. 81) and Bulmershe South Pool, Berks (Griffiths, **3**). Presaddfed also differs from the other four Anglesey lakes in the basin contour factor, and consequently has developed in a different direction. The latter lakes, with their deeper basins and smaller weed-fringes, have evolved into typical Myxophycean waters like those of the similar lakes in Shropshire and Cheshire. The larger and deeper Cumbrian lakes show the same evolution, but to a lesser degree because of the great size of their basins.

The plankton investigations carried out in the Sarek Mountains of Swedish Lappland by Münster Ström again show that on the same rock-area the plankton flora differs from lake to lake, some showing desmid dominance, others diatoms, and one even Myxophyceæ (Ström, **12**, p. 504).

The same investigator's work on Norwegian lakes, most of which are at lower altitudes and many in districts with a good soil-covering, show even more strikingly that the effects of the character of the underlying rock may be completely modified by the other factors of the habitat-complex (Ström, **13**, pp. 2–9). He calls attention to the presence of lakes in Norway both of the "Caledonian" type and of the "Baltic" type, and of "transition forms" between the two (Ström, **13**, p. 43). These conclusions, which can be paralleled in Sweden (Naumann, **7**), in North America (G. M. Smith, **10**, **11**), and, as we have seen, in England also, all tend to show that the terms "Caledonian" and "Baltic" are of ecological and not of distributional significance. There is a Tropical desmid flora, and there are Temperate and Arctic floras, each of which is probably determined broadly by temperature and sunlight ranges as in higher plants. Within each broad division there are habitat differences due to ecological factors, of which initial water-supply, contour of the basin and character of the topography, are the chief dominants. The "Caledonian" plankton is simply the flora which survives in a particular type of habitat-complex, and the "Baltic" in another. It is probable that the former can occur only on areas of ancient rock (but see Harris, **6**, and Atkins & Harris, **1**), whereas the latter might occur anywhere, either on ancient or newer rock.

The transition from one to the other may take two directions. If the basin is fairly deep and steepsided, with a consequently small weed-fringe, the dominance shifts from desmids towards Myxophyceæ, Bacillarieæ (*Tabellaria*, *Asterionella*, *Melosira granulata*, etc.), and Peridinieæ (*Ceratium hirundinella*). If the basin is smaller and less steepsided, with a consequent larger weed-fringe, the dominance tends to shift to Protococcales, together with a desmid flora of the alkaline, organic water type.

These shifts of type are excellently seen in the Anglesey Lakes and Llyn Ogwen, and it is the ecological significance of their developmental tendencies rather than their alga-floral composition, which gives them interest to the phytoplankton ecologist.

In conclusion I wish to thank Mr. W. Palethorpe of Dudley for his kind permission to collect from Llyns Traphwlls and Penrhyn. To Col. Fox-Pitt of Presaddfed I am greatly indebted, not only for permission to examine the lake but for much very useful information. I am much obliged to Mr. P. Bridden, manager of the Holyhead Waterworks Company, who was good enough to place at my disposal an official analysis of the water of Llyn Traphwlls.

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# On the Pollination of *Primula vulgaris* Huds.

By E. M. Marsden-Jones, F.L.S.

(Plate **11** and 1 Text-figure.)

[Read 7th January, 1926.]

## Introduction.

In order to determine with the greatest degree of accuracy the part that day and night flying insects might respectively play in the pollination of *Primula vulgaris*, a series of systematic observations were made by day and by night during the Spring of 1925, and in addition a double experiment under controlled conditions was carried out.

Before detailing these, it may be useful to examine the various arguments which have been brought forward in support of *nocturnal* pollination, and which have been so ably summarized by Miller Christy *. His first point deals with a moth *Cucullia verbasci*, actually caught by one of Darwin's sons in the act of sucking a Cowslip flower. Miller Christy admits this was a unique observation ; it can hardly be brought forward as evidence unless confirmed by further observations by independent observers. The time, moreover, when this insect was seen is not stated.

The second argument depends on the alleged similarity between the Primrose and other night-pollinated flowers. The resemblance appears to exist mainly in the colour of the flower, but it must be pointed out that there are many flowers, both of white and allied shades, which, as far as we know, are not pollinated by night. Taken as an isolated fact, the colour of the flower cannot in itself be regarded as a valid argument in favour of nocturnal pollination. If, however, it could be shown that the Primrose is indeed pollinated by night, then its colour might lend additional support to the hypothesis in question, for I have noted that, even in the mass, the Primrose does not show up well in the dark.

The third point is concerned with the nectar guides, which are said usually to be found in night-pollinated flowers. I am not aware to what flowers Miller Christy refers, but Dallman, in his treatment of the same subject † and quoting the authority of Sprengel, points out that typical moth-flowers are devoid of nectar guides, as, for example, *Silene Otites*, *S. noctiflora*, *S. nutans*, and *Lychnis alba* ; also *Silene maritima* and *S. inflata*, which I have myself observed to be freely visited by Lepidoptera at night.

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* Journ. Linn. Soc., Bot. xlvi. (1922) pp. 134-9.

† Journ. Bot. lix. (1921) p. 344.

The fourth argument concerns the alleged increase of scent at night. My own observations have indicated no appreciable difference by day or night, and it would seem that any difference of this nature would have been more marked than is the case. Miller Christy's experience in the clay-pit was certainly curious, but the fact that the air within the clay-pit would be confined and therefore undisturbed, would seem amply to account for the increase of scent. It is not stated if the clay-pit was visited during the day prior to the evening visit. To prove the point satisfactorily this should have been done.

In connection with this, the following observation is worthy of record. On June 8th, 1925, when on the Downs near Calne, Wiltshire, it was noticed that the scent of *Hippocrepis comosa* was very pronounced in a hollow between two ridges; outside there was no appreciable scent, although the plant was growing just as profusely. When standing on the top of the ridge, the scent could be detected rising from the hollow. The time was 4.50 P.M., the day was very hot, and there was bright sunlight. This phenomenon was verified by three other people who were with me.

## DAY OBSERVATIONS IN THE FIELD.

All observations were made over a considerable area in an open part of a wood sloping towards the south at Potterne in Wiltshire, about two miles S.E. of Devizes. For convenience and clearness the day and night observations are detailed separately. In Pl. **11** are shown the principal insects responsible for the pollination of the Primrose. They were all caught in the act of pollination.

The first observation was on April 8th from 3–4 P.M.* The wind was S.W. and the temperature in the sun at 3.45 P.M was 70° and in the shade at 3.50 P.M. 64°. It was the second warm day in succession, and the afternoon was distinctly favourable. Several insects were on the wing: *Apis mellifica* and *Eristalis tenax* visiting *Anemone nemorosa*, and *Bombus hortorum* and *Bombylius discolor* the Primrose. The Bombylius never rested, but hovered in front of the flowers during the act of pollination. *Bombylius major* was not on the wing.

The second observation was on April 11th from 2.15–3.45 P.M. Wind W.; temperature at 3.15 P.M. 60° in the shade, and at 3.45 P.M. 80° in the sun. When the observations started the sky was overcast, but at 3.30 P.M. it became quite clear †. *Bombus hortorum* and *Bombylius discolor* were again observed visiting, both in fair numbers. *Anthophora pilipes* ♀ was also seen pollinating; it was probably only just on the wing as the specimens were very bright.

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* Greenwich Time and Fahrenheit temperatures are used throughout.

† These details as to weather are given on account of their importance with regard to the prevalence or otherwise of insects on the wing.

The third observation was made on April 17th from 3–4.10 P.M. Wind W.; temperature in the sun at 3.30 P.M., 60°. Bright sunshine lasted throughout the observation, but the wind was cold. Insects seen visiting the Primrose were *Bombus hortorum*, *Anthophora pilipes*, both sexes, and *Bombylius discolor*. In order to obtain an idea of the number of flowers visited in a given time a specimen of *Bombus hortorum* was kept under observation: twenty-nine flowers were seen to be pollinated in succession in two minutes, the bee then flying away. Taking the aggregate of insects visiting, the Primrose was being well worked.

The fourth visit was on April 22nd from 1.50 to 3.5 P.M. Wind S.W.; temperature in the sun at 2.40 P.M., 70°. There was sun during the whole of the observation, but a considerable amount of wind. *Bombus hortorum*, *B. hortorum* var. *Harrisellus*, *Anthophora pilipes*, both sexes, *Bombylius discolor* and *B. major* were seen pollinating, the last insect for the first time this year.

A count was made of the number of flowers visited consecutively by *Bombylius discolor*,—two insects were timed. The first visited twenty-four flowers in three minutes, at the rate of fourteen the first minute, four the second, and six the third. During the second minute it spent some little time cleaning its proboscis; this it did whilst hovering on a flower. The second insect was timed for two minutes and visited eight flowers each minute.

The fifth observation was made on April 25th from 11.30 A.M. to 1.15 P.M. Wind W.; temperature at 11.45 A.M. in sun 62°, at 1.15 P.M. 55°. A sunny morning until 12 o'clock, when it became cold and dull. The insects pollinating the Primrose were *Bombus hortorum*, *Anthophora pilipes* ♀, *Bombylius discolor* and *B. major*. I noticed that, owing to the counter attractions of *Nepeta hederacea* and *Ajuga reptans*, *Bombus hortorum* was not so constant in its visits to the Primrose as it was during the last observation. *Eusphalerum primulæ* was seen for the first time. Three insects were timed visiting; *Bombylius discolor* visited for three minutes consecutively, the first minute twelve flowers, the second eleven, and the third eight. With regard to this insect a point of interest was noticed; it refused two flowers on a short-styled plant that had had their anthers eaten by a slug. *Anthophora pilipes* ♀ was timed for two minutes and visited fourteen flowers in each minute. *Bombylius major* paid seven visits in one minute; this insect, several times when visiting, settled completely on the flower and stopped hovering. I have never seen *B. discolor* do this.

The sixth visit was on May 1st from 1.20 to 2.20 P.M. Wind N.; temperature at 1.40 P.M. 52°, and at 2.5 P.M. 55°. A dull cold afternoon and most unsuitable for insects, especially Bombylii, but it was desirable to include a day of this sort in the observations. From 1.20 to 2.5 P.M. no insect was seen visiting; there were a few Bombi on the wing, mostly small, and two or three specimens of *Bombus agrorum*, which visits the Primrose very seldom. At 2 o'clock the sun came out and the wind dropped, and *Bombylius discolor* appeared and began to pollinate the Primrose. Shortly afterwards *Bombus hortorum* was also pollinating. The favourable conditions lasted only a few minutes, and nothing more was seen. These observations are of particular interest, as they show that even on cold dull days which are frequent at this time of year, insects immediately appear during short sunny intervals and begin to pollinate.

The seventh observation was made on May 5th from 1.25 to 3.15 P.M. Wind S.W.; temperature in the sun at 2.30 P.M., 68°. There was bright sun throughout the observation, but a good deal of wind which was rather cold. On the whole comparatively few insects were on the wing, those observed visiting the Primrose being *Bombus hortorum*, *Bombylius discolor*, *Rhingia campestris*, *Meligethes erythropus*, and *Eusphalerum primulæ*.

The eighth visit was paid on May 12th from 1.25 to 3.10 P.M. Wind S.W.; temperature in the sun at 2.30 P.M., 75°. The Primroses were now past their best but still being visited by *Bombus hortorum*, *Anthophora pilipes* ♀, *Bombylius discolor*, *B. major*, and *Rhingia campestris*. The Bombylii were not so consistent as on the previous observations, now visiting *Nepeta hederacea* as well as the Primrose. Last year I was not altogether satisfied with the observations on *Rhingia campestris*; it is a very shy creature, flying off readily when approached closely and most difficult to follow on the wing. Since then I have spent a considerable amount of time observing it closely. It visits consecutively, although it also has a habit of resting for a longer or shorter period between visits. I saw a specimen visit two short-styled flowers and then a long-styled one in succession; later it visited very freely and went from flower to flower consecutively. It placed its head well into the flower-tube and its proboscis, which is from 5–7 mm. in length, is long enough to reach the anthers of the long-styled form. Sometimes it made a special effort, pushing itself forward when visiting this type of flower. *Rhingia* had two ways of visiting the short-styled form: (*a*) in a legitimate manner, inserting its head well into the entrance of the flower; (*b*) collecting pollen without inserting its head. Often before inserting its proboscis into the long-styled form, it tried to find pollen at the top of the tube.

The last observation was made on May 15th from 11.45 A.M. to 1 P.M. Wind S.E.; temperature at 12.45 P.M., 90° in the sun. Since the last observation the weather had become very hot, and the flowers in consequence were much past their best, but even so *Bombylius discolor* and *Rhingia campestris* were still seen pollinating. *Bombus hortorum* was not seen in any great numbers, but on the way out of the wood, after the observation had ceased, one was seen pollinating. It is noteworthy that on each visit paid to the wood, covering a period of nearly six weeks, *Bombylius discolor* was seen pollinating the Primrose. The length of time spent on day observations was in all twelve and a half hours.

Table I. gives a summary of these observations. The list of insects comprises two Hymenoptera, three Diptera, and two Coleoptera. The two Hymenoptera, *Bombus hortorum* and *Anthophora pilipes*, were very frequent; *Bombus hortorum* var. *Harrisellus* was seen only once. I also saw it once in 1924, when some preliminary observations were made in the same wood *.

TABLE I.—*Summary of Day Observations.*

| *Day.* | *Time.* | *Wind.* | *Temperature.* | | *Insects seen visiting.* |
|---|---|---|---|---|---|
| 1925. | | | Sun. | Shade. | |
| April 8th. | 3–4 P.M. | S.W. | 3.35. 70°. | 3.50. 64°. | *Bombus hortorum, Bombylius discolor.* |
| ,, 11th. | 2.15–3.45 P.M. | W. | 3.45. 80°. | 3.15. 60°. | *Bombus hortorum, Anthophora pilipes, Bombylius discolor.* |
| ,, 17th. | 3–4.10 P.M. | W. | 3.30. 60°. | .... | *Bombus hortorum, Anthophora pilipes, Bombylius discolor.* |
| ,, 22nd. | 1.50–3.5 P.M. | S W. | 2.40. 70°. | .... | *Bombus hortorum, B. hortorum* var. *Harrisellus, Anthophora pilipes, Bombylius major, B. discolor.* |
| ,, 25th. | 11.30 A.M.–1.15 P.M. | W | 11.45. 62°. | 1.15. 55°. | *Bombus hortorum, Anthophora pilipes, Bombylius major, B. discolor, Eusphalerum primulæ.* |
| May 1st. | 1.20–2.20 P.M. | N. | 2.5. 55°. | 1.40. 52°. | *Bombus hortorum, Bombylius discolor.* |
| ,, 5th. | 1.25–3.15 P.M. | S.W. | 2.30. 68°. | .... | *Bombus hortorum, Bombylius discolor, Rhingia campestris, Meligethes erythropus, Eusphalerum primulæ.* |
| ,, 12th. | 1.25–3.10 P.M. | S.W. | 2.30. 75°. | .... | *Bombus hortorum, Anthophora pilipes, Bombylius major, B. discolor, Rhingia campestris.* |
| ,, 15th. | 11.45 A.M.–1 P.M. | S.E. | 12.45. 90°. | .... | *Bombylius discolor, Rhingia campestris.* |

N.B.—Shade Temperature = temperature taken when sun went in; the thermometer was not moved.

The three Diptera, *Bombylius major*, *B. discolor*, and *Rhingia campestris*, were very frequent. Insects with a tongue-length of 10 mm. can pollinate effectually and in a regular manner. All these insects, with the exception of *Rhingia campestris*, in which it is from 5–7 mm., have the required proboscis length, but as its visits are concerned with pollen not nectar, the length of its proboscis does not debar it from being an active agent in pollination. It can reach the anthers of the long-styled forms and the stigma of the short-styled,—these organs stand about 6 mm. below the top of the corolla-tube †.

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* See Proc. Linn. Soc. Lond. 137th Session, 1924–25, p. 28.

† The proboscis of *Rhingia campestris* varies in length from 5–7 mm. An insect with the shorter proboscis pollinates efficiently when its head is inserted into the corolla-tube.

It is on the wing approximately from May 5th onwards and is generally distributed, and visits the later flowers with great frequency. *Bombylius major*, with a tongue-length of 10 mm., is on the wing approximately from March 27th to May 24th, and is found as far north as Perthshire. *B. discolor*, with a tongue-length of from 11–12 mm., and on the wing approximately from March 15th to May 17th, is more or less confined to the Southern Counties, not being found farther north than Oxfordshire *. The Bombylii are most constant visitors, favouring almost exclusively the Primrose; it is only just at the end of its flowering period that they visit other flowers. In Wiltshire, it is called the Primrose-fly.

The two Coleoptera, *Meligethes erythropus* and *Eusphalerum primulæ*, play, I think, little or no part in the pollination of this plant.

## NIGHT OBSERVATIONS IN THE FIELD.

The night observations were made in the same wood. A strong acetylene lamp was used for the work. With it forty or fifty plants could be observed at the same time, and *Forficula auricularia* could be seen in a flower at a distance of four yards. The light was either gently moved in a circle, or suddenly flashed on a patch of plants.

The first observation was on April 9th from 9.20 to 10.20 P.M. Wind S.E.; temperature at 10 P.M., 46°. There was a slight shower for a few minutes at 9.40 P.M., while gentle rain had fallen most of the afternoon, but the evening was fine though the sky was overcast during most of the observation. The moon was full, and it was a most suitable evening for moths. With the exception of the Earwig, *Forficula auricularia*, nothing was visiting the Primrose; one small geometrid was noted on the wing in the wood.

The second observation was on April 11th from 8.30 to 9.30 P.M. Wind W.; temperature at 9 P.M., 45°. It was a clear starlight night. With the exception of *Forficula auricularia* nothing was seen visiting the Primrose. One small noctuid, *Tæniocampa pulverulenta*, was attracted by the light; this was the only moth seen on the wing.

The third visit on April 17th was from 9 to 10 P.M. Wind W.; temperature at 9.45 P.M., 44°. There was no wind and it was a most suitable night for moths. For the first forty minutes, with the exception of *Forficula auricularia*, no insects were seen, then a noctuid crossed the beam of light, hovered round, and flew away. It was not caught in case it should subsequently pollinate, but although kept under observation until it flew right away, at no time did it go near the Primroses.

The fourth observation was on April 20th from 8.20 to 9.20 P.M. Wind N.E.; temperature at 8.50 P.M., 40°. It was a coldish night, but though probably not too cold for moths to be on the wing, none were seen. *Forficula auricularia* was observed in the flowers.

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* G. H. Verrall, 'British Flies,' v. (1909), pp. 496–9.

The fifth observation was made on April 23rd from 8.15 to 8.45 P.M. Wind W.; temperature at 8.45 P.M., 40°. There was rain at 6.45 P.M., and the flowers were still rather wet. No insects were seen.

The sixth observation was on April 24th from 8.45 to 9.30 P.M. Wind W.; temperature at 9.20 P.M., 40°. The flowers were rather damp. It was a clear night—no insects were seen.

The seventh visit was on April 25th from 10.30 to 11.30 P.M. Wind W.; temperature at 11 P.M., 43°. It was a damp evening, with a very slight shower during the observation. Between 11 and 11.30 P.M. four moths were seen, two geometrids and two noctuids. None of these made any attempt to visit the Primroses.

The eighth observation was on April 28th from 11.30 P.M. to 1 A.M. Wind N.; temperature at 12 P.M. 39°, falling to 37° at 12.30 A.M. It was a clear night—moonlight until 12 P.M. There was a cold breeze at times. No insects were seen.

The ninth visit was on May 2nd from 9.40 to 10.40 P.M. Wind W.; temperature at 10.15 P.M., 43°. It was a moonlight night. *Tachyporus solutus* and *Forficula auricularia* were observed in the Primroses, no moths were on the wing.

The tenth observation was on May 6th from 8.30 to 8.50 P.M. Wind E. to S.E.; temperature at 8.50 P.M., 48°. The night was windy. No moths were on the wing. The observation had to be discontinued owing to heavy rain.

The eleventh observation was on May 11th from 1 to 2.45 A.M. Wind N.W.; temperature at 2 A.M., 45°. There was moonlight until 2.15 A.M. One noctuid was seen on the wing, but nothing visiting the Primroses.

The twelfth observation was on May 12th from 2.40 to 4.40 A.M. Wind S.W.; temperature at 3.45 A.M., 48°. The only insect seen visiting was *Meligethes erythropus*. It was an ideal night for moths, but none were seen. The lamp was put out at 3.45 A.M., as it was then possible to see the flowers plainly. It is worth recording that as early as 4.16 A.M. *Bombus agrorum* was seen pollinating *Ajuga reptans* and *Nepeta hederacea*.

The thirteenth visit was also on May 12th from 8.45 to 9.45 P.M. Wind S.W.; temperature at 9.20 P.M., 49°. It was possible to see the nectar guides in the flower till 9 P.M., and the lamp was not used until that hour. No moths were on the wing.

The fourteenth observation was on May 13th from 8.15 to 9.30 P.M. Wind S W.; temperature at 8.45 P.M., 56°. The night was fine and no lamp was used until 9 P.M. The only insect seen visiting the Primrose was *Meligethes erythropus*. A thin-bodied moth, probably a Thorn, was on the wing.

The fifteenth and last observation was made on May 15th from 8.45 to 10 P.M. Wind S.E.; temperature at 9.15 P.M., 62°. On this, as on the two previous occasions, the lamp was not used until 9 P.M., at which time the dark centres of the flowers could still be seen at a distance of five feet. One noctuid was seen on the wing, but nothing visiting the Primroses.

The time spent in observations totalled sixteen hours twenty minutes, and covered the entire night from 8.15 P.M. to 4.40 A.M. After 4.15 A.M. day-flying insects were liable to appear. Several visits were duplicated, not only to observe on nights of varying atmospheric conditions, but in order to spend as much time as possible in the wood during the time when moths would be most likely to be on the wing.

TABLE II.—*Summary of Night Observations.*

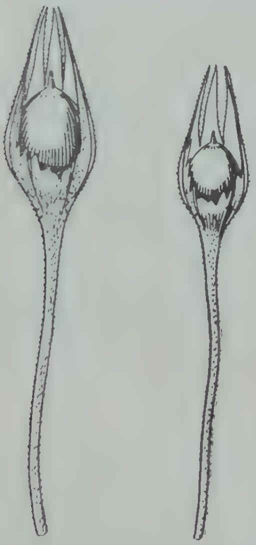
| *Date.* 1925. | *Time.* | *Wind.* | *Temperature.* | *Insects seen visiting.* |
|---|---|---|---|---|
| April 9th. | 9.20–10.20 P.M. | S.E. | 46° | *Forficula auricularia.* |
| „ 11th. | 8.30–9.30 P.M. | W. | 45° | „ „ |
| „ 17th. | 9–10 P.M. | W. | 44° | „ „ |
| „ 20th. | 8.20–9.20 P.M. | N.E. | 40° | „ „ |
| „ 23rd. | 8.15–8.45 P.M. | W. | 40° | No visitors. |
| „ 24th. | 8.45–9.30 P.M. | W. | 40° | „ „ |
| „ 25th. | 10.30–11.30 P.M. | W. | 43° | „ „ |
| „ 28th. | 11.30 P.M.–1 A.M. | N. | 39°–37° | „ „ |
| May 2nd. | 9.40–10.40 P.M. | W. | 43° | *Tachyporus solutus, Forficula auricularia.* |
| „ 6th. | 8.30–8.50 P.M. | E.–S.E. | 48° | No visitors. |
| „ 11th. | 1–2.45 A.M. | N.W. | 45° | „ „ |
| „ 12th. | 2.40–4.40 A.M. | S.W. | 46° | *Meligethes erythropus.* |
| „ 12th. | 8.45–9.45 P.M. | S.W. | 49° | No visitors. |
| „ 13th. | 8.15–9.30 P.M. | S.W. | 56° | *Meligethes erythropus.* |
| „ 15th. | 8.45–10 P.M. | S.E. | 62° | No visitors. |

The observations are summarized in Table II. The insects seen in or on the Primrose were two Coleoptera, *Meligethes erythropus* and *Tachyporus solutus*, and one Orthopteron, *Forficula auricularia*. These insects are of little or no value from a pollinating point of view, and one, *Forficula auricularia*, is distinctly harmful, owing to its eating anthers and stigmas.

## CONTROLLED EXPERIMENTS.

For controlled experiments, Miller Christy suggested that "selection should be made of a number of plants (say, fifty or a hundred) all growing together in natural conditions (preferably in a wood). Just before flowering, all might be 'covered' (by the means usually adopted for preventing insects from obtaining access to and pollinating flowers), and so remain till all or most of the plants were in full flower. Then one half of the plants might be exposed just after dusk and re-covered just before sunrise, while the other half might be exposed just before sunrise and re-covered just before dusk. This might be continued for (say) three days or nights, after which all the plants should remain covered permanently until the time when any seed they may have set should have ripened. If, then, the plants were examined and it was found that those which had been exposed by night only had fruited freely, while those exposed by day only had not, we should have good evidence that the plants are pollinated normally by night-flying moths; or, if the converse were found to be the case, we should know that the large-tongued bees and butterflies which are known to visit the flowers by day suffice to pollinate them adequately, though this appears at present to be impossible, owing to the fewness of their visits. But this method, though it might prove conclusively that the flowers are pollinated normally by night-flying moths, would not show the particular species by which this is effected."*

TEXT-FIG. 1.



Large and small capsules, showing relative size. × 1½.

It was not possible for me to arrange the experiment in the wood where the observations were made, as it is nearly two miles from my house; it was therefore carried out in the orchard. In the early spring a hundred plants were collected in the wood, and planted in two blocks of fifty each,—side by side,—five rows of ten plants, long- and short-styled in alternate rows; in the last row the plants were arranged long- and short-styled forms alternately. Each patch was six feet by three feet. Instead of continuing the experiment for a few days only, it was extended until the plants were out of flower.

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* Journ. Linn. Soc., Bot. xlvi. (1922) pp. 138–139.

TABLE III.

| PLANTS EXPOSED DURING DAY | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **LONG STYLED FORMS** | | | | | | | | | | | TOTALS |
| *Large capsules* | 13 | 3 | 0 | 7 | 8 | 1 | 5 | 2 | 8 | 10 | 57 |
| *Small capsules* | 2 | 2 | 3 | 5 | 2 | 1 | 0 | 1 | 0 | 4 | 20 |
| **SHORT STYLED FORMS** | | | | | | | | | | | |
| *Large capsules* | 5 | 0 | 1 | | 4 | 0 | 1 | 4 | 9 | 6 | 30 |
| *Small capsules.* | 0 | 0 | 1 | | 0 | 0 | 3 | 1 | 0 | 11 | 16 |
| **LONG STYLED FORMS** | | | | | | | | | | | |
| *Large capsules* | 0 | 0 | 10 | 3 | 10 | 6 | 7 | 7 | 12 | 14 | 69 |
| *Small capsules* | 1 | 0 | 7 | 0 | 1 | 4 | 8 | 4 | 1 | 1 | 27 |
| **SHORT STYLED FORMS** | | | | | | | | | | | |
| *Large capsules* | 1 | | 0 | 6 | 8 | | 1 | 0 | 6 | 4 | 26 |
| *Small capsules* | 3 | | 4 | 1 | 0 | | 0 | 2 | 1 | 1 | 12 |
| **LONG & SHORT STYLED FORMS** | | | | | | | | | | | |
| *Large capsules* | 9 | 1 | 6 | 1 | 3 | 2 | 11 | 3 | 12 | 11 | 59 |
| *Small capsules* | 3 | 0 | 9 | 0 | 2 | 0 | 5 | 0 | 7 | 1 | 27 |

Total: Large capsules 241=512·8 per cent.
" Small capsules 102=217 per cent.

The experiment started on the morning of April 12th, when all flowers were picked off both batches. A wooden frame with tiffany over the top was used to cover the plants.

*Day Exposure.*—In the day block the protecting frame was moved at 6 o'clock each morning (from April 19th it became, owing to Summer Time, actually 5 o'clock). The change-over in the evening became gradually later as the nights got longer. The experiment ended on May 23rd.

TABLE IV.

| PLANTS EXPOSED DURING NIGHT | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| LONG STYLED FORMS | | | | | | | | | | | TOTALS |
| *Large capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Small capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SHORT STYLED FORMS | | | | | | | | | | | |
| *Large capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Small capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 4 |
| LONG STYLED FORMS | | | | | | | | | | | |
| *Large capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Small capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| SHORT STYLED FORMS | | | | | | | | | | | |
| *Large capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Small capsules* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LONG & SHORT STYLED FORMS | | | | | | | | | | | |
| *Large capsules* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Small capsules* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Total: Large capsules 0.
" Small capsules 5 = 10·2 per cent.

In making the count of capsules it was found that there were two sorts, one type large and well developed, the other smaller but containing a few good seeds. Text-fig. 1 (p. 375) shows the relative size of the capsules. The large capsule was about 10 mm. long and 6·75 mm. broad, the small one about 7 mm.

long and 5 mm. broad. Table III. (p. 376) gives a plot of capsules produced by the plants exposed during the day. Three plants failed. The total number produced by the forty-seven remaining plants was as follows:—Large capsules 241, small capsules 102. Three plants did not produce capsules. As the experimental plants, compared with the plants in the wood, could not produce nearly so many flowers the result obtained is very satisfactory.

*Night Exposure.*—Table IV. (p. 377) gives a plot of the capsules produced by the plants exposed by night. The result is quite startling in its negativeness.

TABLE V.

| LONG STYLED PLANTS | | | |
|---|---|---|---|
| N°1 | N°2 | N°3 | |
| 0 | 0 | 0 | LARGE CAPSULES |
| 0 | 0 | 0 | SMALL CAPSULES |
| 70 | 31 | 42 | FLOWER STALKS |

| SHORT STYLED PLANTS | | | |
|---|---|---|---|
| N°4 | N°5 | N°6 | |
| 0 | 0 | 0 | LARGE CAPSULES |
| 0 | 0 | 0 | SMALL CAPSULES |
| 64 | 61 | 43 | FLOWER STALKS |

One plant failed; the forty-nine remaining plants produced five capsules only, all small. It is significant also that they were all in a localized part of the patch. There is always, in an experiment of this sort, a chance of error, and it may be assumed that pollination was brought about by a late-flying diurnal insect, or that an early *Bombus* might have visited before the change-over was made in the morning. It has been mentioned that *Bombus agrorum* was seen pollinating *Ajuga reptans* and *Nepeta hederacea* in the wood at 4.16 A.M. on May 12th. The patch of plants chosen for exposure by night was much stronger than those exposed by day. The plants did better and produced many more flowers.

One further experiment was carried out. In Table V. is given the record of a count in which six plants were covered day and night, from April 12th to the end of the flowering-period. All flowers were picked off before the experiment started. No capsules were produced. This when contrasted with the next table proves conclusively that when growing under natural conditions self-pollination does not take place. Table VI. shows the abundance of capsules which were produced by six plants marked at random in the wood while still in flower and left completely exposed. Plant No. 3 agreed very closely in size with the plants used in the experimental patch exposed by day. The number of flower-stalks which produced no capsules given in Tables V. and VI. are only approximate, others no doubt having rotted.

TABLE VI.

| LONG STYLED PLANTS | | | |
|---|---|---|---|
| No 1 | No 2 | No 3 | |
| 32 | 24 | 10 | LARGE CAPSULES |
| 3 | 10 | 3 | SMALL CAPSULES |
| 6 | 30 | 9 | FLOWER STALKS WITH NO CAPSULES |

| SHORT STYLED PLANTS | | | |
|---|---|---|---|
| No 4 | No 5 | No 6 | |
| 36 | 33 | 25 | LARGE CAPSULES |
| 20 | 11 | 10 | SMALL CAPSULES |
| 54 | 18 | 32 | FLOWER STALKS WITH NO CAPSULES |

## CONCLUSION.

On looking through the literature on the pollination of *Primula vulgaris*, it appears to me that in many cases too much mystery has been made of the subject. This apparently has its origin in two statements by Darwin. He says, speaking of the Primrose, "it is surprising how rarely insects can be seen during the day visiting the flowers, but I have occasionally observed small kinds of bees at work; I suppose, therefore, that they are commonly fertilized by nocturnal Lepidoptera." * And again, "the Primrose is never visited (I speak after many years of observation) by the larger humble-bees, and only rarely by the smaller kinds; hence its fertilization must depend almost exclusively on moths." † These are surprising statements to be made by such a very careful observer as Darwin. The common fallacy now prevalent is without doubt built up on his two statements. Avebury states that it "is rarely visited by the larger humble-bees, and not often by the smaller ones. It appears to be mainly fertilized by moths, but is sometimes visited by *Bombus hortorum*." * This appears to be merely Darwin's statement reiterated in slightly different words, and has never been confirmed. Now what are the real facts of the case? In his admirable summary Miller Christy gives a list of insects that visit, and mentions *Bombus hortorum*, *Anthophora pilipes*, *Bombylius major* and *B. discolor* as very frequent visitors †. This statement is borne out by various observers and agrees with what I have myself seen. It is obvious that, compared with the number of flowers produced by the Primrose, the number of visitors does appear small, but this is not an isolated case; the insects observed visiting the British Orchises for instance do not appear to be very frequent, as anyone who has studied them will admit, yet they are regularly pollinated and set abundance of capsules.

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* 'The Different Forms of Flowers,' p. 36.

† *Ibid.* p. 56.

Again, climatic conditions play a large part in the appearance of insects on the wing at the time of year when the Primrose is in flower, but, given favourable conditions even for only a short period, insects are at once on the wing and pollinating. On most days in spring there are such short intervals, and on many, several hours of sunshine. During the whole of my day observations I never went to the wood without seeing insects pollinating; the rapidity with which they visit is also significant.

To turn now to my night observations, they give absolutely negative results, as do the observations of Dallman in Flintshire and Denbighshire ‡. Adding together the time spent by both of us there is a total of twenty-seven hours; it scarcely seems credible that, if moths, as alleged, do play such an important part, one or other of us should not have obtained direct evidence. Night observations must of necessity be made with a light, and the effect this might have on moths must be taken into consideration. On June 11th a test was made on this point, *Lychnis alba* being selected. The lamp was flashed on a moth at a distance of two yards, and the insect was kept in the circle of light during the observation. It visited thirteen flowers in succession, the light having no effect at all. A further observation was made on June 12th; in this case on a moth pollinating *Silene nutans*. The lamp was flashed on the insect at a distance of one yard; eleven flowers were visited in succession; eight pollinated satisfactorily and three visited only for a second or so. Two other moths were subjected to a still closer test, the lamp being about nine inches from them, but they continued to pollinate. It is obvious from these tests, made with the same lamp that was used in the wood, that moths were not deterred from visiting on account of the light.

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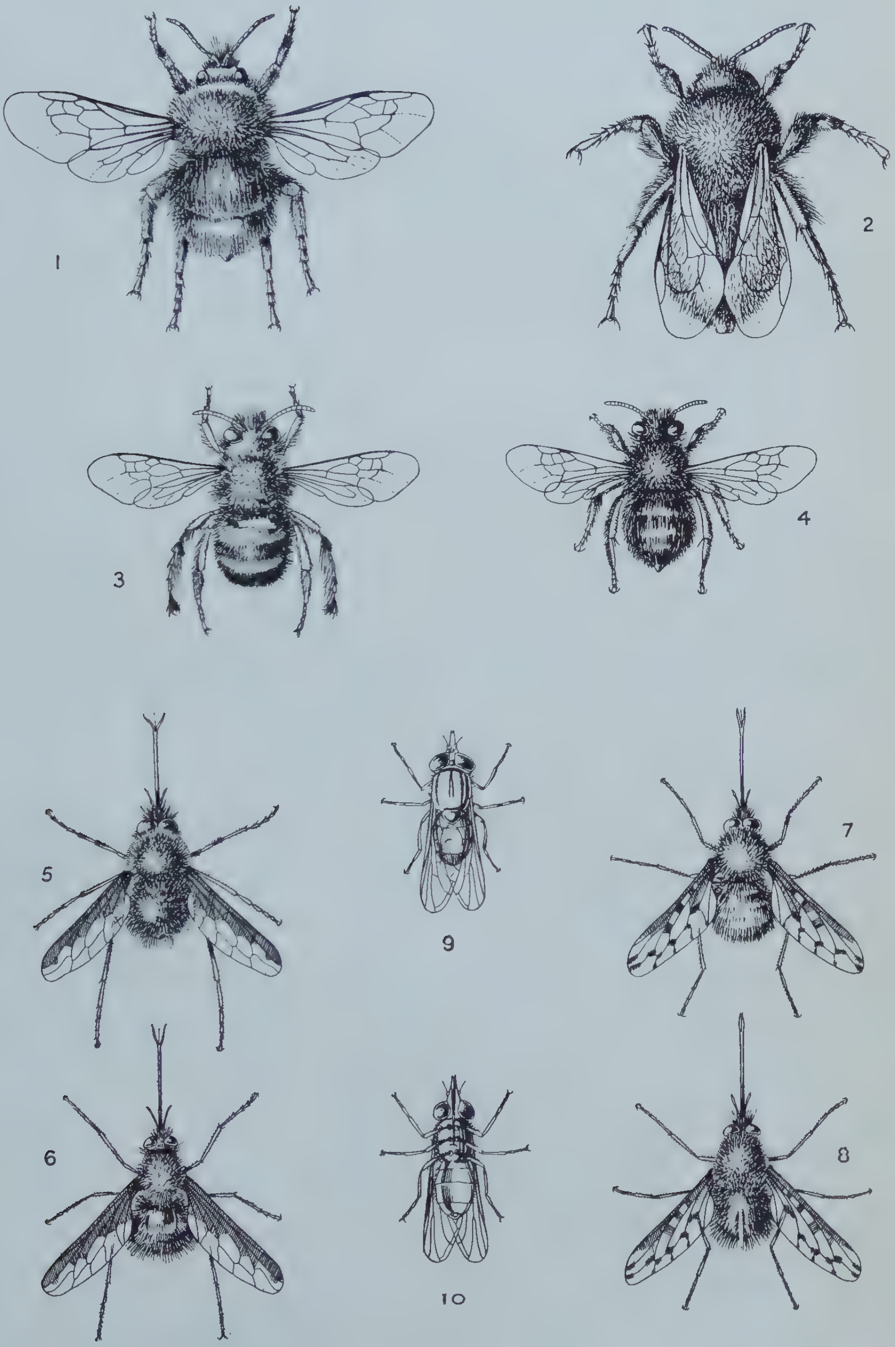
* 'British Flowering Plants,' p. 269.

† Journ. Linn. Soc., Bot. xlvi. (1922) p. 127.

‡ Journ. Bot. lix. (1921) pp. 320–1 and 337–8.



POLLINATION OF PRIMULA VULGARIS Huds.

Comparing the day and night observations in the wood with the controlled experiments, we get direct confirmation. The patch exposed by day fruited well; the patch exposed by night produced only five small capsules, which, when taking all the evidence into consideration, cannot be attributed to nocturnal Lepidoptera.

There is now direct, and experimental evidence, to prove conclusively that diurnal insects actually pollinate the Primrose and pollinate efficiently. This should end all speculation and doubt as to what insects pollination is due, for the present experiments afford no support whatever to the hypothesis that pollination is effected by unknown nocturnal Lepidoptera, for which after all no definite evidence has ever been produced.

I desire to thank Major E. E. Austen, Dr. James Waterston, and Mr. K. G. Blair, of the British Museum (Natural History), for naming the insects; and my friend Mr. A. D. Cotton of Kew for help and advice. I am also greatly indebted to my wife, who accompanied me on all the night observations as well as most of those during the day and took the notes.

## EXPLANATION OF PLATE 11.

Fig. 1. *Bombus hortorum* ♀.
2. *Bombus hortorum* var. *Harrisellus* ♀.
3. *Anthophora pilipes* ♂.
4. *Anthophora pilipes* ♀.
5. *Bombylius major* ♂.
6. *Bombylius major* ♀.
7. *Bombylius discolor* ♂.
8. *Bombylius discolor* ♀.
9. *Rhingia campestris* ♀.
10. *Rhingia campestris* ♀. Ventral view to show proboscis.

# On the Cuticles of some Fossil and Recent Lauraceæ.

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(PLATES **12–14** and 27 Text-figures.)

[Read 18th March, 1926.]

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## INTRODUCTORY.

IN a former paper (Bandulska, 1923) cuticles of certain dicotyledonous leaves from the Bournemouth Eocene were described, but their relationships were not considered. In a later investigation (Bandulska, 1924) the first of these leaves was identified as a species of *Nothofagus*. Part of the present research deals with evidence for the inclusion of a second leaf, which was previously described as *Dicotylophyllum spiculatum*, in the genus *Aniba*. The paper further demonstrates the presence of three other genera belonging to the

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* Thesis approved for the Degree of Doctor of Philosophy in the University of London.

Lauraceæ—*Litsea*, *Neolitsea*, and *Lindera*—in the Bournemouth Eocene Flora. For comparison and correlation with the fossil leaves, twenty-three genera and about fifty species of Lauraceæ have been studied, but the present paper includes detailed descriptions only of those genera of which fossil species are also described. Much fossil material has been collected agreeing in external form and cuticular structure with the four recent genera above mentioned, which seem to have been very common in the Bournemouth Flora. In studying the recent cuticles, a casual inspection impresses one with the differences among the species of a genus; nevertheless when attention is concentrated on the stomatal apparatus, striking similarities become manifest between recent species of the same genus and between fossil and recent forms.

### *Materials and Methods.*

The recent material used in the present investigation was obtained from the British Museum Botanical Department and from Kew. Two methods were pursued in dealing with it. Firstly, fragments of all the species studied were macerated with nitric acid and chlorate of potash, and their cuticles were stripped off, stained and examined for comparison with the fossil cuticles. Secondly, hand and microtome sections were made through the leaves, although this was a matter of great difficulty, owing to the extreme toughness of the leaf texture; the sections, however, were found an invaluable help in interpreting the surface features of the recent and fossil forms. Each cuticle was photographed, and drawn with the aid of a reflecting prism and the diameters of its stomatal apparatus were measured where possible. Measurements of epidermal and venule cells were found to be inconclusive and were not continued. The fossil material was collected by the writer from the Bournemouth cliffs and chines west of the pier, and must therefore be referred to Gardner's "Bournemouth Freshwater Series," which is now considered of Lower Bracklesham age. The methods of preparation of the fossil plants for investigation followed the lines previously described (Bandulska 1923, p. 243). Many unsuccessful attempts were made to obtain sections of the Eocene leaves, but the conclusion was reached that in these leaves no cellular structure remains; the cuticle as distinct from the epidermis has alone become mummified, and hence yields only surface features. Rubbings of the recent leaves were found useful for comparing the external features with those of the fossils.

### *Previous References.*

Very little research has been carried out upon the leaves of Lauraceæ. Solereder (1908, p. 702) briefly describes their epidermis, but says that a detailed investigation of the leaf structure has not yet been made. He says that the lateral walls of the epidermal cells are only rarely undulated, particularly on the upper side of the leaf. This is incorrect, for sinuation of the epidermal walls is a very common feature, and even more frequent on the upper than on the lower surface. Thus out of nine species of *Aniba* examined, four have a sinuate-walled lower epidermis and six have a sinuate-walled upper epidermis. Again, both species of *Laurus* have a sinuate upper and lower epidermis. Other genera including species with sinuate epidermal cells are *Beilschmidea*, *Phœbe*, *Cryptocarya*, *Neolitsea*, and *Lindera*. On the other hand, Solereder's statement that the stomata of the Lauraceæ are accompanied by subsidiary cells one on either side and parallel to the pore has been fully confirmed. They are generally easy to recognize.

Volker Petzold (1907) describes peculiar ridge-like processes on the guard cells of some American Lauraceæ, which I find are also present in several genera from Africa, Eastern Asia, and Ceylon.

Other writers who deal with the morphological characters of Lauraceous leaves give no description of their cuticular structure.

## I. The Genus *Aniba* Aublet, 1775.

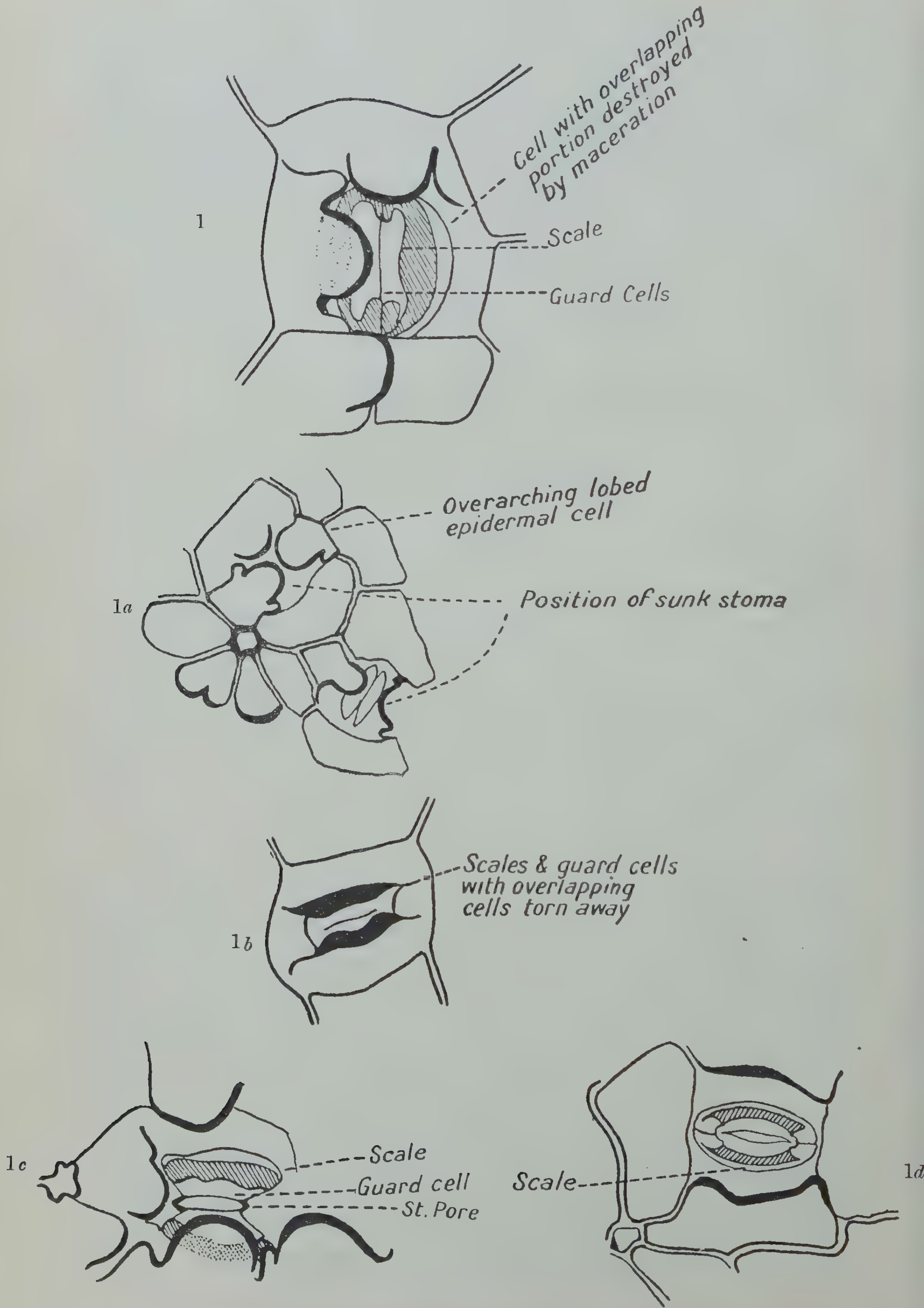
The large genus *Aniba*, numbering some forty-five species, belongs to the group Cryptocaryeæ of the Lauraceæ, and occurs in tropical America, the West Indies, and Ceylon.

The leaves vary in average length from 9 cm. (*A. firmula*) to over 20 cm. in *A. Hostmanniana* and *A. bracteata*. Their width ranges from 3 cm. (*A. firmula*) to over 8 cm. (*A. Hostmanniana*, *A. robusta*, *A. bracteata*). The margin is entire; the venation is pinnate. The number of secondary veins on each side of the midrib varies from six (*A. amazonica*, *A. Ridleyana*) to twelve or fourteen as in *A. lævigata* and *A. Gardneri* respectively, and these make angles with the midrib ranging from 25° or 30° (*A. amazonica*) to 40° or 50° (*A. Gardneri*) or over 60° (*A. bracteata*).

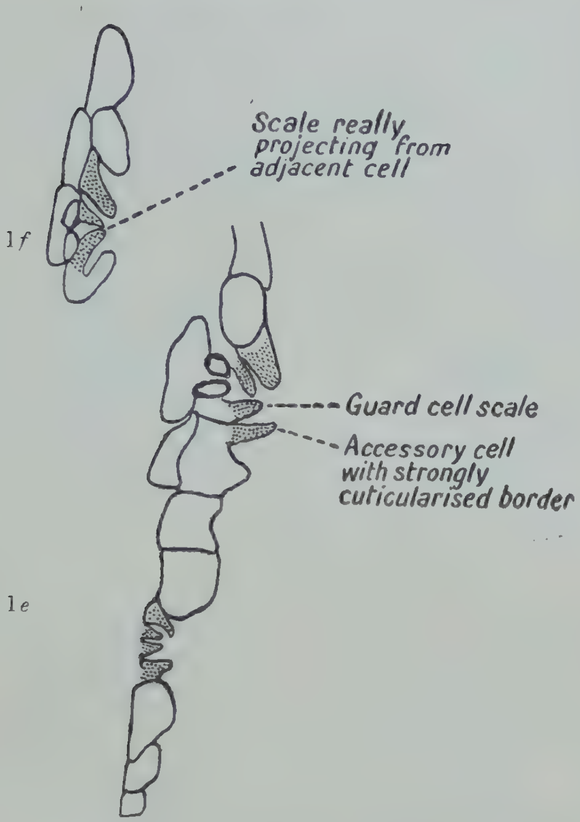
### *a.* **Recent Species.**

### ANIBA GARDNERI (Meissn.) Mez

*Lower Epidermis* (Pl. **12**. figs. 1, 2, 3).—The stomatal apparatus (text-figs. 1, 1 *a–f*) consists of guard cells, usually depressed, with a pair of cuticular ridges or scales, which are attached to adjacent epidermal cells. The cells bordering the stomata arch over them, and the free edges of the former are lobed, each cell having from one to three lobes, the middle lobe being usually the largest. The lobes of opposite cells tend to interlock, so that the guard cells may be entirely or partially hidden. Four such cells commonly surround each pore, but the number of enclosing cells is somewhat variable, and two only may be specialized. Hair-bases (text-fig. 1 *a*), most readily detected with a high power, are numerous and occur close to the pores, and certain cells of these hair-bases may serve as the overarching lobed cells, the free borders of which are strongly cuticularized and stain deeply (see text-fig. 1).


1
Cell with overlapping portion destroyed by maceration
Scale
Guard Cells
1a
Overarching lobed epidermal cell
Position of sunk stoma
1b
Scales & guard cells with overlapping cells torn away
1c
Scale
Guard cell
St. Pore
Scale
1d

TEXT-FIGS. 1, 1 *a–d*.—*Aniba Gardneri*. Guard cells and turned back scales exposed,


Scale really projecting from adjacent cell
1*f*
Guard cell scale
Accessory cell with strongly cuticularised border
1*e*

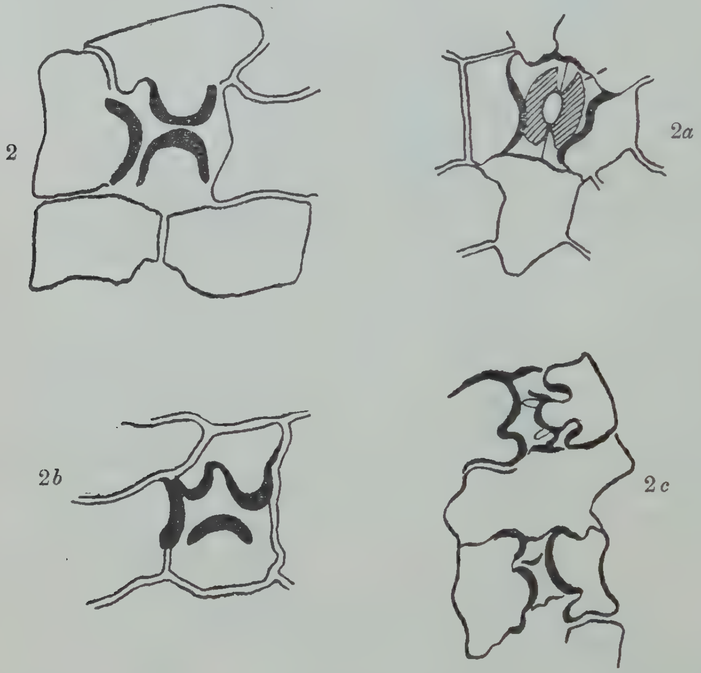
TEXT-FIGS. 1 *e–f*.—Lower epidermis of *A. Gardneri.*

The indentations of the overarching cells may give the pores a cruciform appearance, the opening being like a maltese cross in shape. Stomata and girdling accessory cells form groups of very variable size. Occasionally the overarching cells project but slightly or not at all, and then an open pore bounded by two guard cells with their scales is visible. The stomata sometimes show twinning, that is, two adjacent sets of guard cells are surrounded by one group of overarching cells.

The epidermal parenchyma is fairly abundant and straight-walled. The width of each cell is about three-quarters of its length. The guard cells could not be measured owing to their depressed condition. The average length of the scales is ·0174 mm. parallel to the long axis of the pore, while the average width of a pair across the pore is ·0126 mm.

*Upper Epidermis.*—The parenchyma is thick-walled, sometimes pitted, with slight sinuations in the walls; the elongated venule cells are also sinuate. The epidermal cells are practically isodiametric.

*Vertical Section through the Leaf Epidermis* (text-figs. 1 *e–f*).—In vertical section the depressed guard cells are clearly revealed, overarched by cuticular ridges or scales. The latter are thickened outgrowths arising from the outer border of the guard cell at the junction of guard cell and adjoining epidermal cell, to which they really belong. Much larger overlapping and cuticularized projections of the next adjacent epidermal cells cover in the pore above the scale level.



TEXT-FIGS. 2, 2 *a–c*.—*Aniba firmula,* showing variation in the lobing of the cells bounding the pore.

ANIBA FIRMULA (Nees) Mez

*Lower Epidermis* (Pl. **12**. figs. 4–6).—The guard cells are depressed and bear a pair of scales (see text-fig. 2 *a*). The epidermal cells bordering the stomata arch over them (see text-figs. 2, 2 *a*), and are even more deeply lobed and irregular than in *A. Gardneri*. It is only when the lobes of these opposite overarching cells do not meet, that the sunk guard cells with their scales can be seen (text-fig. 2 *a*). The accessory cells may be one-, two-, or three-lobed. Thus there may be a lobe or a sinus in the middle of each projecting cell, but the lobes are generally more equal in size than in the former species (see text-fig. 2). The abundant epidermal parenchyma has sinuate walls, and bears hair-bases : these occur also on the venules. This species has thus the same general epidermal construction as *A. Gardneri*, differing from it mainly in that the epidermal walls are sinuate, and the two accessory cells are usually more definitely specialized as interlocking and pore-protecting structures, whereas in *A. Gardneri*, although two alone are very common, the number girdling the pore may be three, four, or even six. The width of the ordinary epidermal cells is about three-quarters of their length. The scales have an average length of ·011 mm., and the average width of a pair is ·019 mm. In this species the interlocking by the accessory cells is closer than in *A. Gardneri*, hence the space between two accessory cells is less.

*Upper Epidermis.*—The cell walls are sinuate, as are also the walls of the ill-defined venule cells. The width of the epidermal cells is rather less than three-quarters of their length.

### ANIBA LÆVIGATA (Meissn.) Mez

*Lower Epidermis* (Pl. **12**. figs. 7, 8).—The stomatal apparatus consists of lobed accessory cells projecting over depressed guard cells; adjacent cells below the former bear a pair of scales the average length of which is ·016 mm., also projecting over the guard cells. The accessory cells may be one-lobed or two-lobed with a groove in the middle, but the majority have one large middle lobe and two small lateral ones. All the lobes have their free border thickened. The amount of interlocking produced by the projection of opposite accessory cells is very variable, and may completely conceal or entirely expose the scales. Of the four cells which surround the depressed guard cells, two at least are sharply distinguished by the lobing, which, however, may be found in three or even all four of the enclosing cells though it is most obvious in two opposite ones. The bifurcation of the accessory cells, seen here and there in this species, obtains very generally in the fossil form *A. spiculata*, while inequality of size of opposite accessory cells is a marked feature both in the recent and fossil species. The orientation of the guard cells and their pore is not always the same as that of the opening produced by the girdling accessory cells; the former may be obliquely under the surface opening or be actually at right angles to it, though usually there is parallelism between the two. The epidermal parenchyma has straight or very slightly sinuate walls. The venules bear small hair-bases.

*Upper Epidermis.*—Straight-walled or very slightly sinuate parenchyma constitutes the upper epidermis with a meshwork of ill-defined venules spread over its surface.

### ANIBA RIDLEYANA Mez

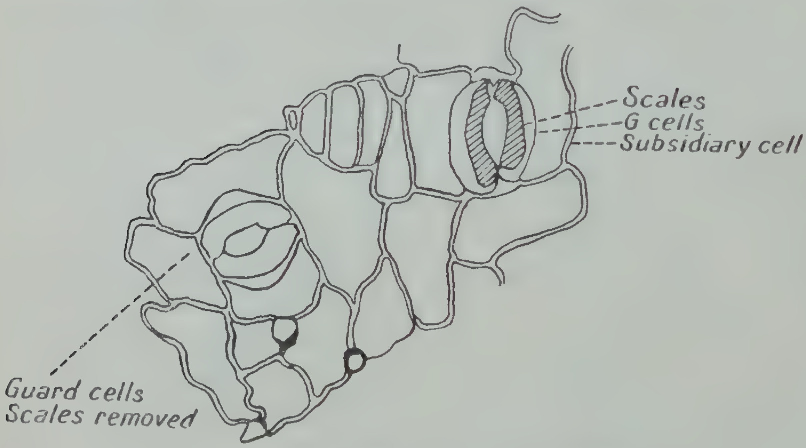
*Lower Epidermis* (Pl. **12**. figs. 9, 10).—The stomatal apparatus consists of delicate scale-bearing guard cells bordered by four to seven undifferentiated epidermal cells. Subjacent epidermal cells frequently contain spicules which may also border the scales. The latter are very large, their average length being ·0202 mm., while the average width of a pair is also ·0202 mm.

The parenchyma cells are thick and practically straight-walled. Occasionally a single sinuation can be seen. A few hair-bases occur among them. Where two parenchyma cells occur parallel to the long axis of the pore, they are very unequal in size.

*Upper Epidermis.*—The cells are thick, straight-walled and polygonal, with here and there a cell showing a sinuation.

### ANIBA HOSTMANNIANA (Nees) Mez

*Lower Epidermis* (Pl. **12**. figs. 11, 12).—The stomatal apparatus is composed of a pair of crescent-shaped guard cells, partially or entirely covered by a pair of scales, which may be unequal in size (text-fig. 3). The guard cells are best seen when the scales have been removed by maceration. The average length of the scales is ·0178 mm., while the average width of a pair is ·0174 mm. Four unequal epidermal cells bound the pore, and two of these may have a median sinus facing the guard cells.



TEXT-FIG. 3.—*Aniba Hostmanniana* (Nees).

The parenchyma is slightly sinuate with numerous hair-bases. The venules spread over the surface bear hair-bases. They form a meshwork which is either quadrangular or polygonal, the angle made by intersecting venules being often but not always a right angle.

*Upper Epidermis.*—The majority of the cells have sinuate walls, but many are practically straight-walled. Hair-bases occur among the cells.

### ANIBA ROBUSTA (Klotz & Karst.) Mez (B.M. Coll. 1758).

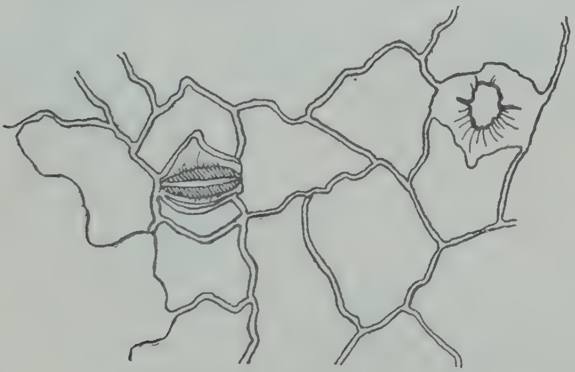
*Lower Epidermis* (Pl. **12**. figs. 13, 14).—The stomatal apparatus consists of guard cells, over each of which is a large scale, which must be removed by maceration to reveal them. Here and there, the scales show on their upper surface two or three sharp, prong-like, simple or bifurcate spicular outgrowths, the points of the prongs turned away from the pore. Four to six epidermal cells border the stomata, and those of opposite sides usually vary much in size. The scales are very large, and this character seems to coincide with the fact that the guard cells are not sunk below the surface, as it was observed also in *A. Ridleyana.* The scales have an average length of ·0214 mm., while the average width of a pair is ·0206 mm.

The parenchyma is thick and straight-walled and the venules are very thick-walled.

*Upper Epidermis.*—The cells are intensely thick and straight-walled, and many are pitted.

ANIBA BRACTEATA Mez (B.M. Coll. 5254).

*Lower Epidermis* (Pl. **12.** figs. 15, 16).—The scale-bearing guard cells are enclosed by a pair of lobed accessory cells (see text-fig. 4), one of which is larger than the other. Both are disposed parallel to the long axis of the pore and may meet at the poles, and owing to their lobing the pore may appear diamond-shaped (text-fig. 4). The diameter of the two accessory cells and pore is much greater at right angles to the long axis of the pore than parallel to it.



TEXT-FIG. 4.—*Aniba bracteata.*

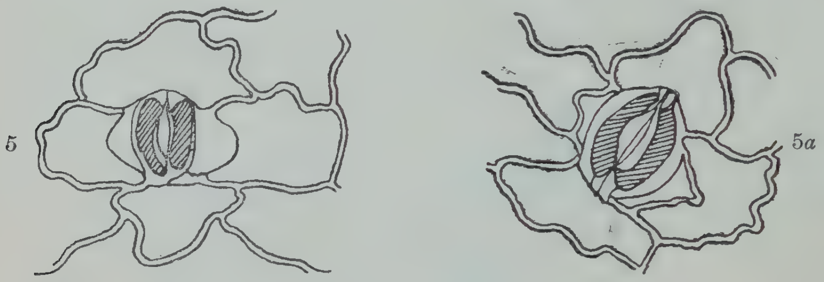
Spicular outgrowths occur under the scales and form a margin round some of them, and when the scales are removed by maceration an irregular jagged pore is seen, spicule bordered, surrounded by pale thin-walled guard cells whose junctions are never clear, with two V-shaped accessory cells. This spicule-bordered pore is seen also in *Aniba Ridleyana.* Minute hair-bases occur at intervals.

The epidermal parenchyma is sinuate, the venules are thick-walled. The scales have an average length of ·022 mm., and a pair has an average width of ·014 mm.

*Upper Epidermis.*—The parenchyma is sinuate and crossed by a few narrow venules. It bears a few hair-bases.

ANIBA AMAZONICA (Meissn.) Mez

*Lower Epidermis* (Pl. **12**. figs. 17, 18).—The guard cells have thickened rims bordering the pore. Large scales project over them, flush with the surface (see text-figs. 5, 5 *a*), and have an average length of ·017 mm., while the average width of a pair is also ·017 mm. Two or four epidermal cells surround the hardly visible guard cells. Two of the girdling cells disposed parallel to the long axis of the pore are somewhat more definitely specialized, staining a little more deeply etc. These are markedly unequal in size and occasionally project slightly over the scales. Often one of these cells or sometimes both are V-shaped (text-fig. 5 *a*), the sinus facing the scales and being wide and shallow.



TEXT-FIGS. 5, 5*a*.—*Aniba amazonica* (Nees), showing V-shaped sinus.

The epidermal parenchyma is abundant, sinuate, and bears small hair-bases.

*Upper Epidermis.*—The cells have thick sinuate walls.

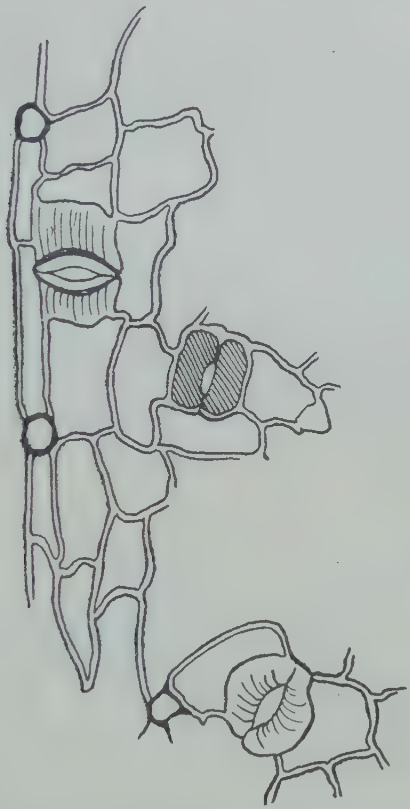
ANIBA DESERTORUM (Nees) Mez, var. GLABRATA (B.M. Coll. 2719).

*Lower Epidermis* (Pl. **12**. figs. 19, 20).—A pair of unequal epidermal cells is disposed parallel to a pore, bordering which is a pair of scales, so large that they may completely hide the guard cells (text-fig. 6) to which they are attached. Where infrequently the scales are vertical, the guard cells are dimly revealed. The scales average ·0152 mm. in length, while the average width of a pair is ·0172 mm. The bordering epidermal cells are commonly four, two parallel and two at right angles to the long axis of the pore, but the number shows some variation.

One or more of the bordering epidermal cells may have a wide and shallow sinus facing the pore and thus tend to be somewhat V-shaped or bilobed, and occasionally these accessory cells project a little over the guard cells with their scales.

The most interesting feature of this species is that spicules occur in a few of the accessory cells, guard cells, and epidermal parenchyma, similar in character to those of *A. spiculata* but fewer and more tenuous (text-fig. 6).

The parenchyma is almost straight-walled, but in other respects it much resembles that of *A. amazonica.* Hair-bases are numerous, among the epidermal cells and on the venules, formed of three to six cells which may constitute the ordinary parenchyma or form the accessory cells of the stomata.



Text-fig. 6.—*Aniba desertorum* Nees, var. *glabrata,* showing spicular ridges.

*Upper Epidermis.*—This is composed of thick-walled sinuate parenchyma packed with delicate spicules. There are no hair-bases on the upper surface. The walls are less sinuate than those of *A. amazonica.*

### *General Characters of* Aniba *Cuticles.*

The stomata, which are restricted to the lower surface, are usually depressed and the guard cells more or less concealed by scales or cuticular projections which appear in surface view to arise on the upper surface of the guard cells. These project over and conceal the latter and more or less cover in the pore (text-figs. 1–6). Two or four (rarely more) accessory cells differing in size, shape, and reaction to stain, overarch and surround the stomata, and of these, the two parallel to the long axis of the pore show more differentiation than the pair disposed at right angles to them, and the former pair alone may in some cases completely girdle the pore. Their free edge is strongly thickened (*A. Gardneri*). They are usually bilobed (*A. lævigata*) or they may be one- to three-lobed (*A. Gardneri*, *A. firmula*). The sinus may be rounded and shallow or deep and angular, and when angular gives a cruciform appearance to the pore.

The lower epidermal parenchyma may be straight-walled (*A. Gardneri*, *A. lævigata, A. desertorum, A. Ridleyana, A. robusta*) or the cell walls may show sinuations (*A. firmula, A. amazonica, A. Hostmanniana*). Spicules may occur sporadically in these epidermal cells (*A. desertorum*). Venules spread over the surface as a quadrangular meshwork, the angles of the mesh being frequently almost right angles. Owing to the depression of the stomata it was not possible to measure the guard cells accurately, but the length of the accessory cells, and the width of a pair of these across the pore, and the diameters of the scale-containing space between the two, were found to be in close agreement in most of the species investigated.

The upper epidermal parenchyma may be sinuate, while the lower epidermis of the same species has straight walls (*A. Gardneri*), or both upper and lower epidermis may be straight-walled (*A. Ridleyana*). Thus this feature is not of specific value.

### *b.* Fossil Species.

ANIBA SPICULATA Bandulska

* (*Dicotylophyllum spiculatum* Bandulska, 1923, pp. 244–247.)

*Occurrence.* Middle Eocene of Bournemouth, Bournemouth Freshwater Series ; between Middle and Alum Chines.

In 1923 a second specimen of this species was found, which showed the external form more completely than in the original specimen, and fragments of cuticle are fairly common.

*External Characters* (Pl. **13**. fig. 25).—Leaf simple, lanceolate, elliptical ; apex missing ; base missing ; margin entire with one slight sinuation ; surface covered with tough cuticle. Venation pinnate with strong midrib and well-marked alternate secondaries, five on the left side and four on the right side making an average angle of 69°. Length of portion present 8·1 cm. Width of leaf 4·6 cm.

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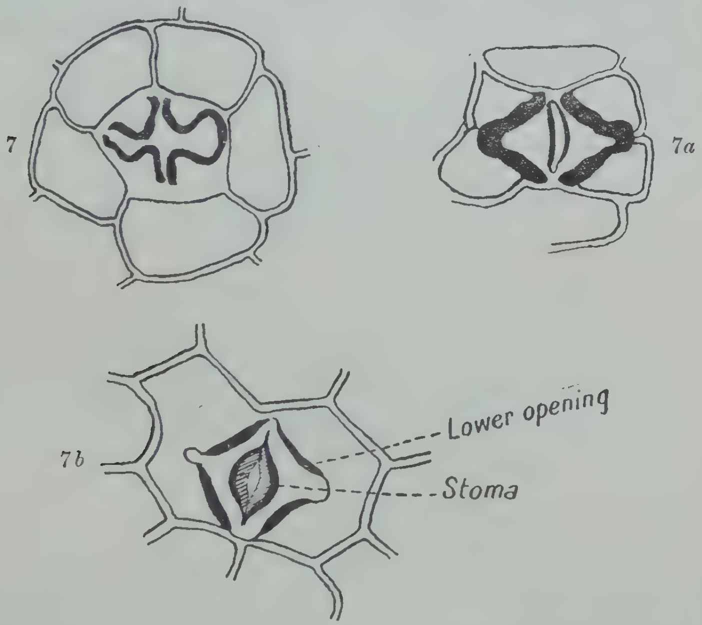
* In an earlier paper (Bandulska, 1923) I proposed the name *Dicotylophyllum* for fossil dicotyledonous leaves of doubtful affinity, overlooking the fact that this name had already been used by Saporta in a more restricted sense for certain leaves from the Urgonian of Portugal (Saporta, 1894, p. 147). The name is therefore originally Saporta's, but it may be more usefully employed in the extended sense suggested in my paper. It would therefore seem better to employ the non-committal term *Phyllites* in cases where the affinities of the leaf are unknown. Of the three species described by me as *Dicotylophyllum*, one has since been referred to *Nothofagus* (*N. Stopesæ* Bandulska, 1924, p. 433), and one is here referred to *Aniba*. The other (Bandulska, 1923, p. 247) must still for the present be called *Dicotylophyllum sinuatum*.

*Lower Epidermis* (Pl. **12**. figs. 21–24).—The stomata, which are entirely restricted to the lower surface, are depressed and overarched by very lobed accessory cells unequal in size, which (text-figs. 7, 7 *a–b*) bound a pore that is irregular but frequently cruciform (text-fig. 7 *b*). The lobing of the accessory cells is very variable and the lobes themselves have a deeply staining border (text-fig. 7 *a*). There is often a deep groove in the middle of each opposite cell of a pair parallel to the long axis of the pore so that the cells are two-lobed and the pore cruciform (text-fig. 7 *b*), or one lobe only may be clearly seen. This was also observed in the first specimen of *A. spiculata* (Bandulska, 1923, pl. 20. fig. 6). The present leaf, however, is in better preservation and part of the actual guard cells and their pores can be seen. The poral rim bears a pair of scales upon it (text-fig. 7 *b*). The epidermal parenchyma is tough, straight and intensely thick-walled, and its individual cells are very asymmetric. Spicular ridges are abundant in all the cells of the lower surface. A meshwork of venules crosses the epidermis.



Text-figs. 7, 7 *a–b*.—*Aniba spiculata.* Overlapping portions macerated away showing stomata with suggestion of scales.

*Upper Epidermis.*—This consists of thick, straight-walled parenchyma. The fossil is more xerophytic than any of the recent species of *Aniba*.

*Summary.*—An investigation of the characters of *Aniba spiculata* shows that in external form and venation the fossil leaf resembles several recent species of *Aniba*; the "shoulder" seen just below the apex in the first fossil specimen (see Bandulska 1923, text-fig. 1, p. 245) is found also in *A. lævigata*, and the curved midrib and tough cuticle of the fossil are in agreement with the recent genus, but these data alone are insufficient for identification. The comparative structure of the cuticles, however, reveals their close relationship. The fossil agrees with recent forms in the following characters:—

(1) The stomata are depressed and restricted to the lower surface.
(2) The guard cells as seen from above bear scales bordering the pore.
(3) Lobed accessory epidermal cells are present which arch over the depressed guard cells.
(4) The lobes of the overarching accessory epidermal cells have a very thickened and deeply staining border.
(5) The lobes are usually two in number (e. g. *A. amazonica*, *A. lævigata*, *A. desertorum*, *A. Hostmanniana*).
(6) The sinus is angular, giving a cruciform effect to the pore (*A. desertorum*).
(7) Opposite accessory cells show marked inequality in size, and may or may not unite to close in the pore at the ends of the long axes.
(8) Spicules occur in some of the accessory cells bordering the pore and in the lower and upper parenchyma in some of the recent species (*A. desertorum*, *A. robusta*), similar in character to those which are a marked feature of *A. spiculata*, but in the former they are less developed.
(9) The upper epidermis is comprised of very thick-walled cells.

From the evidence this fossil leaf appears to belong to the genus *Aniba*, and I propose therefore to call it *Aniba spiculata*. I believe it to be specifically distinct, but to approach most nearly to *A. Gardneri*, *A. lævigata*, and *A. firmula*.

## II. THE GENUS *NEOLITSEA*.

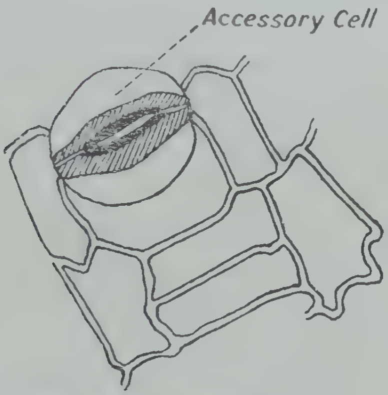
*Neolitsea*, which was originally instituted as a subgenus of *Litsea*, was raised to generic rank by Merrill (1911), who is followed by more recent authors.

Recent *Neolitsea* leaves are ovate-elliptical, oblong-lanceolate or sickle-shaped, with an acute or acuminate sometimes slightly curved apex. They range in length from 9 cm. to over 12 cm., and their average width is about 3 cm. In some species two large secondary veins arise together close to the base of the midrib (*N. formosa*, *N. triplinervia*, *N. zeylanica*). This is by no means always the case, and it is not seen in *N. apoensis* nor always in *N. zeylanica*. The secondary veins apart from the two described may be few or numerous, alternate or almost paired. The angles they make with the midrib range from 20° to 45°. The genus is distributed through the Philippine Isles, Java and other isles of the Indo-Malay Archipelago.

### *a.* Recent Species.

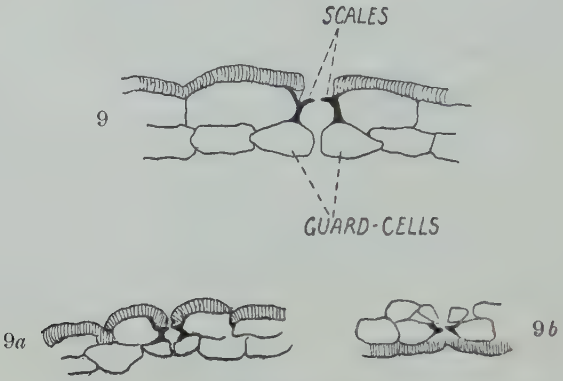
NEOLITSEA APOENSIS Elm. (B.M. Herb. 13849) Philippines.

*Lower Epidermis* (Pl. **13**. fig. 26).—The stomatal apparatus consists of a pair of accessory cells one of which is frequently larger than the other with a very thickly cutinized wall, disposed above and parallel to the small delicate guard cells. Only rarely are the junctions of the guard cells or even their outer walls clearly seen, but the poral rim persists and bears scale-like cuticular ridges, and very infrequently, two tenuous strands of thickening pass from these to the poles (text-fig. 8). The scales arise at the junction of epidermal cell and guard cell and project over the poral rim. One of the accessory cells may be bluntly triangular, its base parallel to the pore. Owing to the usual collapse of the common wall of guard cell and accessory cell, the stomata look extremely broad. Commonly four ordinary epidermal cells surround the stoma, two parallel to the long axis and two at right angles. This number is, however, not always preserved and the surrounding cells and stomata give some evidence that they are the products of successive divisions of an original mother cell, in which case the surrounding epidermal cells would be true subsidiary cells. The cuticle of the lower surface and the venules have sinuate walls. Hair-bases, each formed of a central deeply staining thick-walled rim, surrounded by about five radiating cells, are numerous.



TEXT-FIG. 8.—*Neolitsea apoensis.*

*Upper Epidermis.*—The cuticle consists of sinuate parenchyma crossed by venules bearing hair-bases.



TEXT-FIGS. 9, 9 *a–b.*—*Neolitsea apoensis.* Vertical sections.

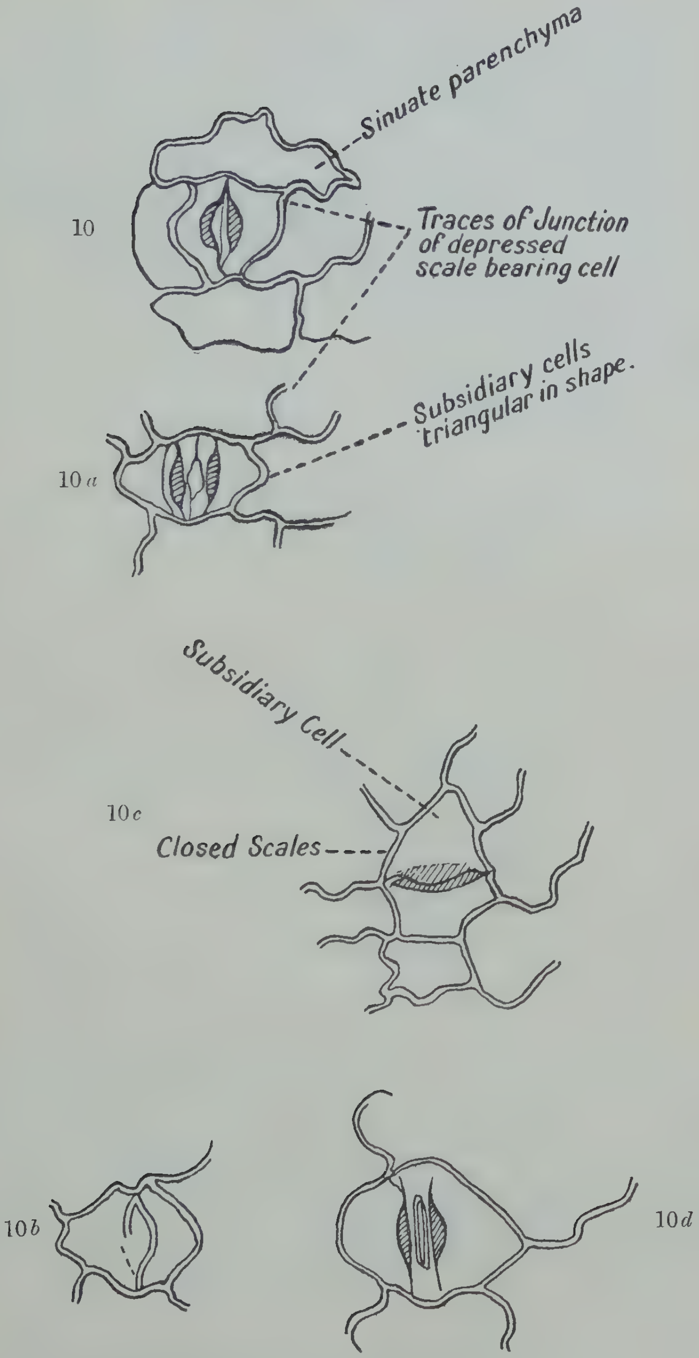
*Vertical Section* (text-figs. 9, 9 *a–b*).—This shows the very depressed and small guard cells, with scales overarched by accessory cells.

NEOLITSEA FORMOSA Moore (B.M. Herb. 2227).

*Lower Epidermis* (Pl. **13**. figs. 27, 28).—The stomatal apparatus consists of a pair of somewhat triangular subsidiary cells whose slightly rounded apices are at right angles to the pore which they surround (text-figs. 10, 10 *a–c*). Frequently the apex of one cell is more elongated and acute than that of the other (text-fig. 10 *d*). Their junctions are easily over-macerated, and therefore are only visible here and there, and whereas the rest of the epidermal parenchyma stains deeply, the subsidiary cells only stain faintly. Rarely is the outline of the guard cells visible from the surface; as in so many other genera of this family they are depressed, but their pore is visible and is rimmed by a pair of scales (text-figs. 10, 10 *a*), which themselves are often torn away, leaving then an oblong tear which narrows slightly at each end, and may be very ragged (text-fig. 10 *b*). Where the material is less macerated, the scales themselves are seen to be continued into a pair of parallel ridges (text-fig. 10 *a*). Very infrequently the junction of the two guard cells may be seen between the scales, surrounding a narrow opening with a slightly thickened rim (text-figs. 10, 10 *a–d*). Here and there an epidermal cell is disposed parallel to the subsidiary cell in such a way as to suggest that it is its mother cell.

A few hair-bases or the bases of secretory cells occur amongst the sinuate parenchyma, and have very thickened radial walls and a thickened rim.

*Upper Epidermis.*—The sinuate parenchyma consists of smaller cells with thicker walls, and bears a few hair-bases.


Sinuate parenchyma
10
Traces of Junction of depressed scale bearing cell
10 a
Subsidiary cells triangular in shape.
Subsidiary Cell
10 c
Closed Scales
10 b
10 d

TEXT-FIGS. 10, 10 *a–d.—Neolitsea formosa.*

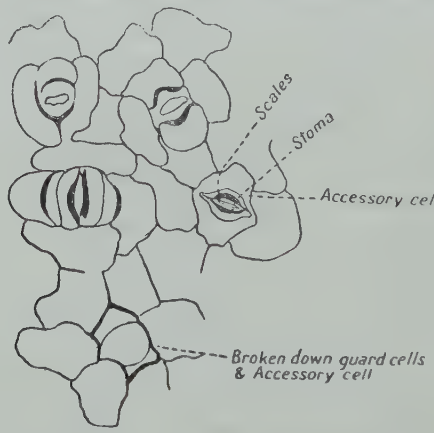
NEOLITSEA TRIPLINERVIA Blume (B.M. Herb. 866).

*Lower Epidermis* (Pl. **13**. figs. 29, 30).—The guard cells, which bear a pair of scales projecting above them, are invisible from the surface; they are encircled by a pair of subsidiary cells, not staining readily, whose horizontal elongation and somewhat triangular shape are characteristic of the genus. The stomata are generally enclosed by four or five sinuate-walled epidermal cells, two of which are disposed parallel to the long axis of the pore, and two at right angles to this when four are present. Their walls bordering the subsidiary cells are thickened, and they show evidence of being the products of division of an original mother cell. A few hair-bases similar to those of *N. apoensis* are to be seen.

The upper surface bears more numerous hair-bases. It is composed of sinuate parenchyma.

NEOLITSEA ZEYLANICA Nees

*Lower Epidermis* (Pl. **13**. figs. 31, 32).—The stomatal apparatus (text-fig. 11) consists of fragile guard cells, whose outer walls are easily overmacerated. A pair of cuticular ridges or scales, which are readily removed, grow out of them and project over the poral rim, which becomes very ragged when the scales are destroyed by maceration. The guard cells are bounded and overarched by a pair of accessory cells with very thickly cutinized upper walls, which stain but faintly, and readily break down (text-fig. 11). One or both of these accessory cells is triangular in shape with its base resting on the guard cells, and when the wall between the guard cell and accessory cell breaks down the stomata become very much horizontally elongated, and may appear triangular.

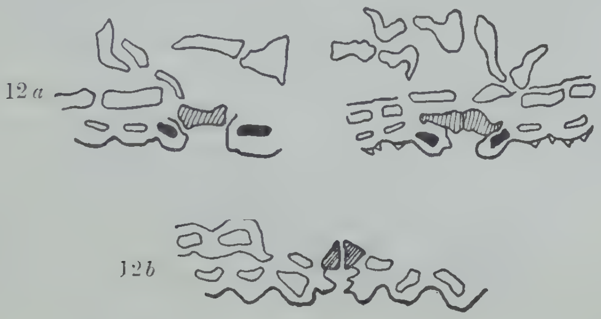


TEXT-FIG. 11.—*Neolitsea zeylanica* Nees.

Stomata and accessory cells are surrounded by four or five ordinary, deeply staining epidermal cells, often four in number, rarely three, and two of these often have definitely cuticularized walls bordering the stomata.

The parenchyma has walls with a hint of sinuation, and there are numerous hair-bases interspersed, each consisting of a central thickened rim, bordered by about five radiating cells. A rectangular meshwork of ill-defined venules is spread over the surface, and most of the hair-bases are associated with these venules.

*Upper Epidermis.*—The walls of the upper epidermal parenchyma are thick, pitted and sinuate. A meshwork of venules on which small hair-bases or the bases of secretory cells are situated, is spread over the surface.



TEXT-FIGS. 12 *a*, *b*.—*Neolitsea zeylanica.* Vertical sections of lower epidermis.

*Vertical Section* (text-figs. 12 *a*, *b*).—This reveals the deeply sunk guard cells with overarching accessory cells. Text-fig. 12 *b* shows the cuticular outgrowth of the adjacent epidermal cell which forms the scale.

### *General Characters of* Neolitsea *Cuticles.*

The cuticle of the lower surface, to which the stomata are restricted, is delicate. The generally depressed guard cells are bounded by a pair of accessory cells, of which one is usually larger than the other, parallel to their long axes, and both guard cells and accessory cells readily break down. The poral rim has projecting over it, a pair of scales or cuticular ridges arising from the junction of adjacent epidermal cell and guard cell which exhibit more resistance to maceration, but these also may be destroyed and leave a very ragged pore bounded only by accessory cells, which do not stain so readily as the remaining parenchyma. Here and there one accessory cell only, instead of a pair, may be seen. The common wall between accessory cell and guard cell is frequently destroyed, and a very wide horizontally elongated triangular appearance is then presented by the stomata which sometimes show twinning.

The epidermal cells have more or less sinuate walls. Four epidermal cells most frequently surround the stomatal apparatus, two parallel to the long axis and two at right angles to this. This number is, however, not always maintained, and the surrounding cells, in places, give evidence that they are products of successive divisions of an original mother cell, whose ultimate segments are the guard cells.

Venules form a meshwork separating the stomata into groups. The cuticle of the upper surface is more resistant and the walls of the epidermal cells are sinuate.

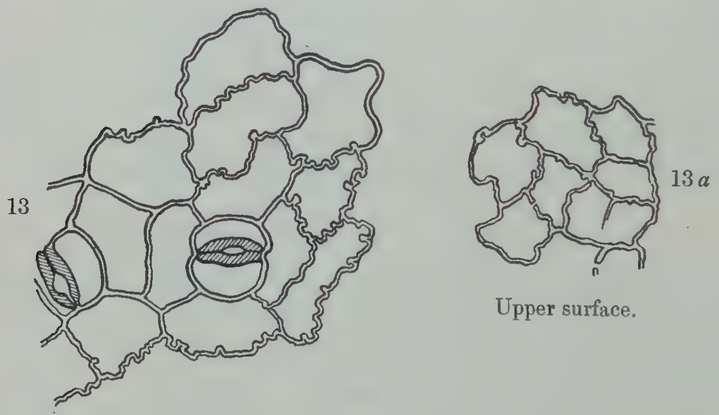
There is but little definite distinction between the cuticles of *Neolitsea* species. The differences are mainly those of texture and degree of sinuation. *Neolitsea triplinervia* has almost straight walls, or slightly sinuate walls in its lower epidermis, while *N. formosa* exhibits a marked degree of sinuation.

### *b.* Fossil Species.

NEOLITSEA GARDNERI sp. nov.

*Occurrence.* Eocene of Bournemouth (B.M.G.D. V. 12647, V. 12650).

*External Appearance* (Pl. **13**. fig. 33).—Two specimens of this leaf were identified in the collection of Bournemouth plants made by Mr. Starkie Gardner, after whom I have much pleasure in naming this species. Leaf simple ; ovate-lanceolate, elliptical ; apex missing ; margin entire to slightly undulating ; midrib strongly marked with about seven secondaries on each side close together, some almost paired. These make angles of 40° to 70° with the midrib. Blade length 10·6 cm. to 11·9 cm. Blade width 3·5 cm. Stalk 2·1 cm.



Lower surface.

Upper surface.

TEXT-FIGS. 13, 13 *a*.—*Neolitsea Gardneri.*

*Lower Epidermis* (Pl. **13**. figs. 34, 35).—The stomata are restricted to this surface. The guard cells are delicate and often destroyed, though occasionally their junctions can be seen. Projecting from the poral rims, pairs of scales stand erect, and close in the pores or lie back like the open leaves of a book and expose them (text-fig. 13). Tenuous lines of cuticularization connect them to the poles of the poral axes. The pore and invisible guard cells are bordered by deeply staining accessory cells, one of which may be larger than the other. Surrounding the guard cells and accessory cells are deeply staining epidermal cells which vary in number from four (the usual number) to six. The stomata may show twinning, that is, two stomata may be encircled by one set of girdling parenchyma. The parenchyma is thick-walled and shows much sinuation and the walls have little knob-like thickenings. There is an absence of hair-bases, and this is probably to be correlated with the thickness of the cuticle.

*Upper Epidermis.*—This is made up entirely of thick-walled sinuate parenchyma with bead-like thickenings on the walls (text-fig. 13 *a*).

*Summary.*—The external form and the cuticle of the fossil leaf named *Neolitsea Gardneri* indicates its close relationship to recent *Neolitsea* species.

The fossil and recent forms agree in the following cuticular characters:—

The stomata are restricted to the lower surface. The guard cells are fragile and readily destroyed. They are depressed and are themselves practically invisible. Scales or cuticular ridges project above them and border the poral rim; these scales are more resistant, but when destroyed they leave a ragged pore. The pore is bounded by two delicate readily over-macerated accessory cells, one of which is larger than the other, and broader than long. Four to six epidermal cells girdle each stomatal group, and appear to be also of the nature of accessory cells giving evidence of origin from one mother cell by successive divisions (text-figs. 10, 11, 13).

The epidermal cells of both upper and under surface have sinuate walls.

In the fossil these cells can be differentially stained, but differential staining is not characteristic of those cells in recent species.

*Neolitsea Gardneri* is more xerophytic than any of the recent species examined, both upper and lower epidermis being tougher.

## III. The Genus *Litsea*.

This genus, including about one hundred species, is mainly represented in the Indo-Malay Archipelago. The leaves are exceedingly variable in size in the different species, ranging from 31 cm. in length and 9 cm. in width to 3·5 cm. in length and 0·5 cm. in width. In shape they are ovate-elliptical (*L. sebifera, L. fuscata*) to lanceolate (*L. Stocksii*), with acute or obtuse apex, and entire margin. The leaves are generally penninerved, but the basal secondaries may be almost paired (*L. Stocksii* and *L. fuscata*). The angle made by the secondary veins with the midribs differs according to the position of the vein in the leaf, the lower veins making usually smaller angles than the upper ones. The number of secondary veins ranges from five to twelve.

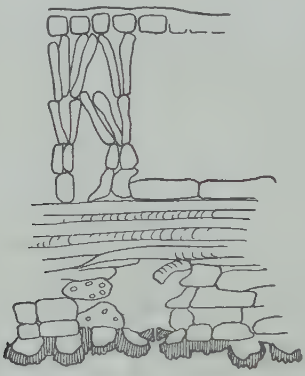
*Litsea* and *Neolitsea* show such a small amount of vegetative distinction that external leaf-form alone would probably never serve as a criterion of distinction between them.

On the whole, the leaves are less leathery in texture than in most other genera of this family, but the upper surface is tougher than the under one.

### *a.* Recent Species.

LITSEA STOCKSII Hook. fil. var. GLABRATA, No. 18921.

*Lower Epidermis* (Pl. **13**. figs. 36, 37).—Heavily cutinized accessory cells project over the pore like a pair of jaws and beneath these are scaly cuticular outgrowths on the poral rim of the deeply sunk guard cells, which are unequal in size, one of them being sometimes triangular.



TEXT-FIG. 14.—*Litsea Stocksii.* Vertical section.

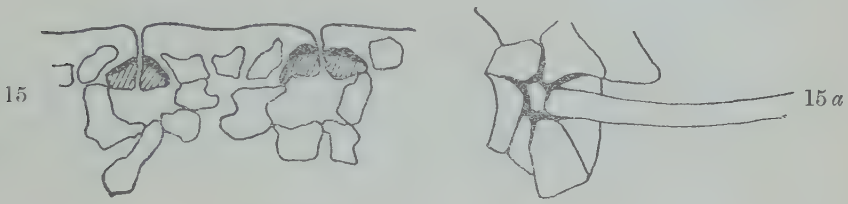
Four to six papillose epidermal cells encircle each stomatal group. Venules about three cells wide form a close meshwork and where they intersect, here and there, rosette-like projections of papillose cells are seen. The venule cells are bead-like or moniliform.

*Upper Epidermis.*—This consists of straight thick-walled parenchyma.

*Vertical Section* (text-fig. 14).

LITSEA FUSCATA Meissn., No. 413.

*Lower Epidermis* (Pl. **13**. figs. 38, 39).—The stomata are scattered irregularly and are very abundant. The guard cells in vertical section are triangular in shape (text-fig. 15). They are depressed and covered by a very thick layer of cutin which dips down between them and masks their shape, leaving a narrow scale-rimmed opening, but their scales are frequently destroyed by maceration. The triangular guard cells are bordered by a ring of undifferentiated epidermal cells, which slightly overlap them. Hair-bases frequently bearing long unicellular sclerenchymatous hairs (see text-fig. 15 *a*) are abundant on the numerous venules which form a polygonal or quadrangular meshwork, and probably the slight development of scales is to be correlated with the presence of these hairs.



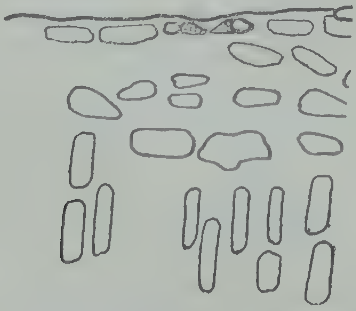
TEXT-FIGS. 15, 15 *a*.—*Litsea fuscata.*

*Upper Epidermis.*—The cells are thick-walled and hairless with occasional slight sinuations in the walls.

*Vertical Section.*—This reveals the thickness of the cutin, which dips down leaving slit-like openings, at the base of which are depressed triangular guard cells overarched by accessory cells (text-fig. 15).

LITSEA SEBIFERA Pers., var. TOMENTOSA Hook. fil.

*Lower Epidermis* (Pl. **13**. figs. 40, 41).—The stomata show no definite grouping but are scattered irregularly between the straight-walled parenchyma which is readily over-macerated. The guard cells are slightly longer than broad; their junctions and their outer walls are very easily over-macerated, while the poral rim is markedly cutinized, the cutinizations slightly projecting in places to form short and narrow scale-like ridges where the pore is widest. Each guard cell is itself bordered by an epidermal



TEXT-FIG. 16.—*Litsea sebifera.* Vertical section.

cell parallel to its long axis, and with the breaking down of the intervening wall the fusion of the two gives a false appearance of extreme breadth to the stomata, and now and then a triangular appearance at right angles to the pore. The pore is somewhat variable in length as well as width. Four or five epidermal cells encircle the guard cells and their parallel accessory cells. Thick-walled tubular hair-bases occur on the venules and less frequently on the epidermal parenchyma.

*Upper Epidermis.*—This consists of thin uniform parenchyma crossed by venules bearing hair-bases.

*Vertical Section.*—The guard cells are very slightly below the level of a pair of cells which partly overlaps but does not conceal them, and both are covered with cuticle dipping in between them. The epidermal cells are very thin-walled and hardly stain (text-fig. 16).

### *General Characters of the Cuticles of* Litsea.

The cuticles of the lower surface are extremely delicate. The stomata are very abundant and are protected by hairs (*L. fuscata*), hair-bases, or papillose cells (*L. Stocksii*), and show no definite grouping. The guard cells may be very depressed (*L. fuscata* and *L. Stocksii*) or may not (*L. sebifera*). They are bordered by specialized or unspecialized accessory cells, unequal in size, which may partially or completely overarch them, or as in *L. sebifera* may be parallel to them. The common wall between guard cell and accessory cell readily breaks down and gives an effect of horizontal elongation to the stomata, which often exhibit a triangular appearance owing to one or both accessory cells having an acute apex at right angles to the long axis of the pore which they bound. The poral rim may be thickly cutinized (*L. sebifera*), or the cutinizations may be further developed to form narrow scales (*L. fuscata*). Four to six epidermal cells close in each stomatal group, and it would seem that the accessory and guard cells are the ultimate products of segmentation from a mother cell which first cut off the encircling cells. When no well-defined accessory cell is disposed parallel to the length of the guard cell, two of the encircling epidermal cells meet in such a way as to make an acute angle, at right angles to the long axis of the guard cells.

The parenchyma of the lower surface of the species examined is thin and straight-walled, while that of the upper surface has much thicker walls, in which slight sinuations are occasionally visible. On both surfaces the venules form a meshwork, which may be wide- or close-meshed and polygonal or quadrangular. Hairs or hair-bases are always more abundant upon these venules than elsewhere. There does not seem to be any definite anatomical distinction between the cuticles of *Litsea* and *Neolitsea*; the cells of the latter, however, are usually more markedly sinuate.

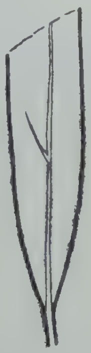
### *b.* **Fossil Species.**

LITSEA EDWARDSI sp. nov.

*Occurrence.* Bournemouth Beds, Eocene.

*Locality.* Durley Chine, Bournemouth, and Cliffs between Alum and Durley Chines.

*External Characters* (Pl. **13**. fig. 45, text-fig. 17).—Leaf simple, lanceolate, base cuneate ; apex missing ; margin entire, with slight curve towards distal end. Length (incomplete), width 1·4 cm. Cuticle not tough. Midrib prominent, bearing one secondary vein in one specimen and three secondaries in another. Petiole 5 cm. long, very slender.

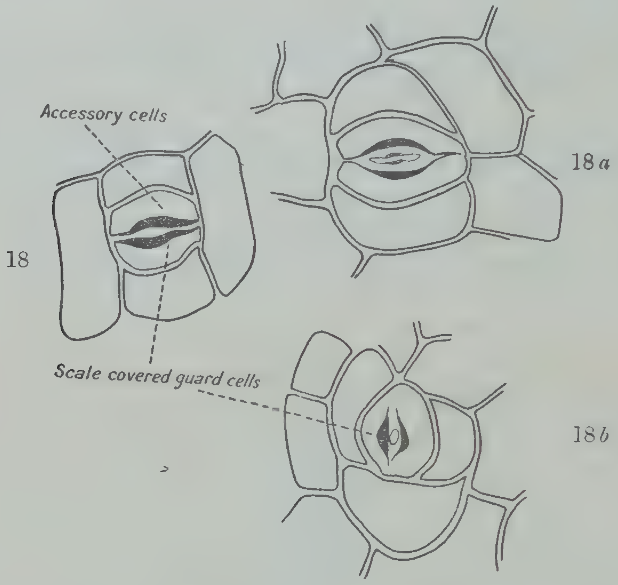


TEXT-FIG. 17.—*Litsea Edwardsi.*

*Lower Epidermis* (Pl. **13**. figs. 42, 42 *a*, 43).—The parenchyma cells are thin-walled and occasionally sinuate ; the approximately rectangular venules bear a few hair-bases, consisting of five to seven radiating cells with a thickened border surrounding a central hair.

The stomata, which have no definite grouping, show occasional twinning. The guard cells are sometimes very asymmetrical and slightly longer than broad, with very delicate outer walls, and junctions which are sometimes broken down. The poral rim appears strongly cutinized, with a pair of narrow upstanding scales or ridges from which slight cuticular ridges proceed to the poles. One of the guard cells is frequently triangular with its apex at right angles to the long axis of the stoma. This appearance is really due to fusion with an accessory cell. One or rarely two epidermal cells close in the guard cells above and below. These cells, with the parallel accessory cells, are evidently the results of a series of segmentations from a common mother cell (text-figs. 18, 18 *a*–*b*). Thus all are true subsidiary cells.

The venule cells differ very little from the rest of the parenchyma, being only somewhat narrower.



Text-figs. 18, 18 *a–b.—Litsea Edwardsi.*

*Upper Epidermis* (Pl. **13**. fig. 14).—This consists of sinuate parenchyma, crossed by a rectangular meshwork of venules whose component cells have also sinuate walls. They bear a few small hair-bases at infrequent intervals.

Litsea hirsuta sp. nov.

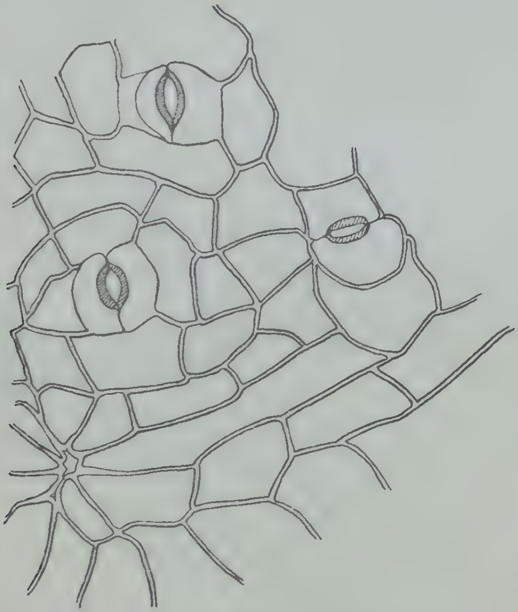
*Occurrence.* Bournemouth Beds, Eocene (B.M.G.D. V. 12652–3).

*Locality.* Bournemouth.

*External Characters* (Pl. **14**. fig. 46).—Leaf slightly obovate, spatulate; a very small portion of the apex is missing; margin slightly and irregularly sinuate to undulating; secondary veins alternating or almost paired. Ten secondaries occur on the left side of the midrib. These secondaries show distinct forking, one bifurcating halfway between midrib and edge (about 2·7 cm. from the edge), the remainder 4·5 mm. from the margin. They make angles with the midrib ranging between 31° and 40°. Length of blade 14 cm. to 8·2 cm., stalk 0·5 cm. Width of blade 6·4 cm. to 4 cm.

*Lower Epidermis* (Pl. **14**. figs. 47, 48).—Stomata are confined to the lower surface. They consist of thin-walled guard cells unequal in size, much elongated at right angles to the pore, and bearing scales. Their apices at right angles to the pore are frequently acutely triangular or one only may form a triangle; they are undoubtedly accessory cells which have become confluent with the guard cells. The polar junctions of the guard cells are mostly destroyed, or unstained, but the poral rim bears a very definite pair of scales or cuticular ridges which may be open or closed, and from which cuticular strands can sometimes be seen passing to the delicate polar junctions (text-fig. 19).

The epidermal parenchyma is straight-walled and the cells show much variability in size and shape. From two to four or five epidermal cells form a group round each stoma and here and there give evidence of the apical type of segmentation. The cuticle bears vast numbers of hair-bases mainly seated on the venules, which are two or three cells wide. Each hair-base is constituted of seven to nine cells with thickened radial walls radiating from a thick-walled central somewhat irregular opening.



TEXT-FIG. 19.—*Litsea hirsuta.* Lower epidermis.

*Upper Epidermis.*—This consists of small parenchyma with straight and thick walls; minute hair-bases occur on the venules.

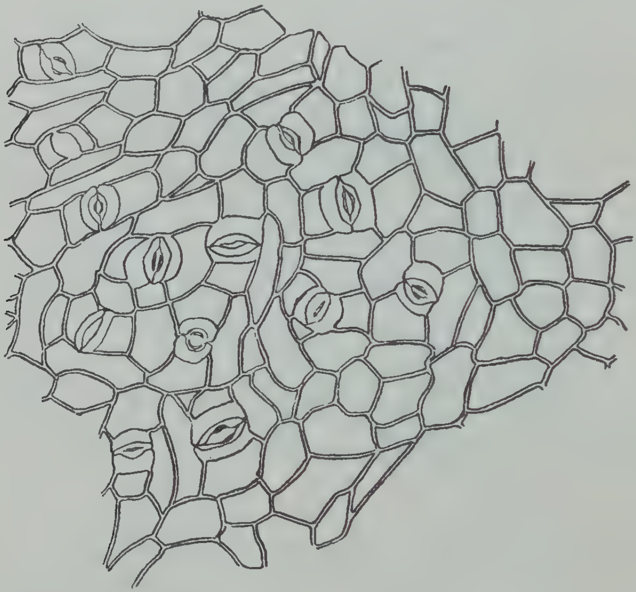
LITSEA BOURNENSIS sp. nov.

*Occurrence.* Bournemouth Beds, Eocene (B.M.G.D. V. 12646).

One specimen of this leaf with its outline complete was found in the Gardner Collection from Bournemouth, and numerous fragments also yielding well-preserved cuticle were found *in situ* by the writer.

*External Characters* (Pl. **14.** fig. 49).—Leaf simple, lanceolate, apex somewhat blunt; margin entire; venation pinnate, midrib well marked, but all laterals except one obliterated. The secondary vein present makes an angle of 27° with the midrib. Length of blade 6·7 cm., length of stalk ·9 cm., width of blade 1·2 cm.

*Lower Epidermis* (Pl. **14**. figs. 50, 51).—Stomata are confined to the lower surface. The guard cells are in some instances apparently unequal in size; the rim is bordered by short and narrow scales (text-fig. 20), while the rest of the poral rim is only slightly cutinized. The guard cells are enclosed by three, four or five epidermal cells two of which are parallel to their long axes, and are presumably derived by segmentation from a common mother cell.



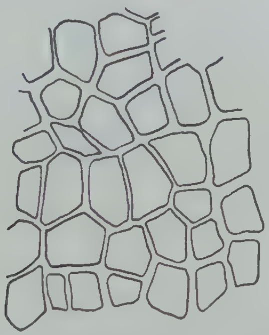
TEXT-FIG. 20.—*Litsea bournensis*. Lower epidermis.

The stomata are very numerous, and apart from the accessory cells which surround them, there is only a thick-walled parenchyma. Occasionally the outer walls of the guard cells, or one of them, is broken down, fusion with the accessory cell parallel to its long axis then taking place as in the recent species *L. sebifera*. Stomata and parenchyma are enclosed in a plexus of thick-walled venules, on which a very few hair-bases are to be seen, which consist of about eight radiating cells surrounding a central space. Correlated with the poor development of hairs, is the toughness of the walls of the epidermal cells.

*Upper Epidermis* (text-fig. 21).—This is made up of thick-walled parenchyma without stomata.

*Summary.*—An investigation of the cuticular structure of the fossils named *Litsea Edwardsi*, *L. hirsuta*, and *L. bournensis* shows that they must be referred to the Lauraceæ and placed in the genus *Litsea.* The cuticles of the fossil and recent species agree in their delicacy. The stomatal apparatus is always characterized by great breadth and by the presence of paired unequal, often triangular accessory cells, overlapping depressed scale-bearing guard cells. Other points in common are the segmentation of these accessory cells and their encircling epidermal cells from a common mother cell. There is a constant tendency for the outer walls of the guard cells and their junctions to break down, the cells then fusing.

Evidence from the cuticles alone would perhaps scarcely suffice for identification with actual living species, and, moreover, there are small differences which fully warrant the use of separate names for the various fossil forms.



TEXT-FIG. 21.—*Litsea bournensis.* Upper epidermis.

*Litsea Edwardsi* has a very delicate cuticle with few hair-bases, the upper epidermal cells have sinuate walls, and the stomata tend to be more asymmetrical. *Litsea hirsuta* and *L. bournensis* have straight-walled epidermal cells. The first bears very numerous hairs, and the second has a tougher cuticle with much thicker walls both of epidermal and venule cells as well as more numerous stomata.

## IV. THE GENUS *LINDERA.*

*Lindera* is represented at the present time mainly in Eastern Asia and America. Of the species investigated, *L. Oldhami* is from Formosa, *L. Prattii*, *L. Meissneri*, *L. megaphylla*, *L. pulcherrima*, *L. strychnifolia*, and *L. rubronervia* from China, and *L. præcox* from Japan.

The leaves vary in average length from 14 cm. (*L. megaphylla*, *L. Prattii*) to 6 cm. (*L. pulcherrima*); their width varies from 7 cm. (*L. Prattii*) to 1 cm. They are simple and oblong or elliptical (*L. Oldhami*) to obovate (*L. megaphylla*), delicate or coriaceous and are penninerved or three- to five-ribbed. *Lindera rubronervia* may be penni- or tri-nerved (text-figs. 22, 23), as is also *L. strychnifolia.* The number of secondary veins ranges from three (*Lindera rufa*) to seven (*L. Meissneri*) or to ten or twelve (*L. Oldhami*, *L. megaphylla*). The veins, except the basal ones, make angles with the mid-rib varying from 40° to 60°, but the basal veins make angles of about 30° with the midrib.

### *a.* Recent Species.

LINDERA MEGAPHYLLA Hemsl.

*Lower Epidermis* (Pl. **14.** figs. 52, 53).—This is a most beautiful form. The stomata are depressed and each is encircled by about ten tiny differentially staining moniliform epidermal cells. Within this ring a varying number of depressed accessory cells, resulting apparently from tangential division of the ring cells, project over still lower guard cells which are delicate and easily destroyed by maceration. Where present they are seen to bear a pair of large scales arising as in other genera from the junction of accessory and guard cells, with cuticular prolongations to the poles; the prolongations stain very faintly or not at all, while the scales themselves stain much more deeply. The whole effect is much like that of the diatom *Pseudonavicella* lying in a cavity. The epidermal cells are small and papillate. The venule cells are also papillate, and the edge of a venule may present a frilled apearance.

*Upper Epidermis.*—This consists of sinuate parenchyma.

LINDERA OLDHAMI Hemsl.

*Lower Epidermis* (Pl. **14.** figs. 54, 55).—This is easily over-macerated. The stomatal apparatus consists of a ring of seven to eight accessory cells slightly raised above the level of the surrounding parenchyma. These cells are somewhat variable in size, and some project more than others; they girdle a pore in which small depressed guard cells can be seen at a lower level. These exhibit the characteristic *Pseudonavicella*-like outline with pale polar extremities and bear the small scales or cuticular ridges seen also in other species of this genus.

The somewhat sinuate epidermal parenchyma is spread over with a network of venules which bear hair-bases, to which in some cases unicellular acicular hairs are still attached.

*Upper Epidermis.*—This is composed of parenchyma with sinuate walls, and is delicate and easily over-macerated.

This cuticle resembles that of *Lindera megaphylla* in the grouping of the accessory cells, but the epidermal parenchyma of *L. Oldhami* is non-papillate.

LINDERA MEISSNERI King (B.M. Herb. 17228).

*Lower Epidermis* (Pl. **14.** figs. 56, 57).—Very delicate stomata are enclosed by papillate epidermal cells. The stomata consist of pairs of faintly staining accessory cells, or one only, parallel to the exceedingly thin-walled non-staining guard cells whose pore is rimmed by a pair of scales, which are elongated and narrow and attached by minute cuticular thickenings. These cuticular ridges are slightly swollen and nodulose, and sometimes beak-like terminally. The outline of the stomata with their scales and their ridge-like continuations is somewhat like *Pseudonavicella*. The scales are seen open, half open or closed.

The accessory cells stain but faintly and their junction with the guard cells is exceedingly delicate and often breaks down, making the stomata very elongated across the pore.

Well-defined venules about six cells wide make a rectangular meshwork enclosing papillate epidermal cells and stomata.

*Upper Epidermis.*—This consists of straight-walled non-papillate parenchyma crossed by a rectangular meshwork of venules.

### LINDERA PULCHERRIMA Benth.

*Lower Epidermis* (Pl. **14**. fig. 58).—A close meshwork of venules bears numerous hair-bases and many long unicellular tapering sclerenchymatous hairs, slightly bulbous at the base. The stomata are depressed and the guard cells concealed by paired accessory cells which project right over them leaving a slit-like opening. At a lower focus the scaly ridges on the guard cells can be seen. Two narrow epidermal cells are disposed parallel to the over-arching accessory cells, *i.e.* parallel to the slit, while one cell, usually considerably larger, closes in the stomatal group at right angles to the long axis of the pore. The epidermal cells are not papillate as in *L. Meissneri*. Their walls are very slightly sinuate or quite straight.

*Upper Epidermis.*—This is composed of very sinuately walled parenchyma with a meshwork of venules bearing hair-bases and hairs similar to those of the lower epidermis.

### LINDERA PRATTII Gamble (B.M. Herb. 809).

*Lower Epidermis* (Pl. **14**. figs. 59, 60).—The stomatal apparatus consists of a pair of triangular asymmetrical accessory cells jaw-like in form, which may or may not completely project over the guard cells. In the former case they have a narrow elongated slit, through which the poral rim can be seen, bordered by a pair of thick and wide cuticular ridges or scales with narrow unstaining prolongations which approximate at the poles, giving again the *Pseudonavicella*-like appearance. The epidermal parenchyma is thin and straight-walled, and bears numerous large, torn cells which are apparently secretory, each slightly raised and surrounded by a ring of narrower cells at a lower level.

*Upper Epidermis.*—The upper epidermis is built up of straight-walled cells which have secretory cells among them similar to those seen in the lower epidermis. The adjacent cells are rich in contents and stain differently.

LINDERA PRÆCOX Blume

*Lower Epidermis* (Pl. **14**. fig. 61).—The stomatal apparatus consists of a pair of guard cells with faintly staining, or unstained nodulose or tumid ends which easily break down. They bear large scales or ridges which arch over them and cover them in, so that at a high focus neither guard cells nor pore are visible. On focussing downwards their outline is rather like that of *Pseudonavicella*. These guard cells are bordered by a pair of delicate accessory cells not taking up stain. Often one of these cells is larger than the other, and may be triangular, but it is more usually oblong, or even rounded.

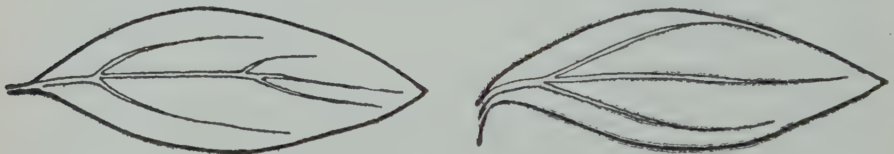
The triangular character is seen commonly in *Litsea*, in this genus only occasionally. Moreover, *Lindera* cuticles are distinguished from those of *Litsea* by the greater elongation of the guard cells and their more generally defined *Pseudonavicella*-like outline with tumid or nodulose unstaining junctions.

Four to five epidermal cells surround the guard and accessory cells and stain fairly deeply. The epidermal parenchyma is sinuate.

*Upper Epidermis.*—This consists of straight-walled parenchyma readily destroyed by maceration.

LINDERA RUBRONERVIA Gamble (B.M. Herb. 1637). (Text-figs. 22, 23.)

*Lower Epidermis* (Pl. **14**. figs. 62, 63).—Very delicate, somewhat depressed stomata bear deeply staining ridges or scales, which may stand erect or be closed. The thin unstained walls of the guard cells and their junctions and the cuticular linear prolongations of the scales are visible on careful focussing. One or a pair of delicate and transparent accessory cells borders the guard cells, and may overarch them and close in the pore, which now and then shows a thick *Pseudonavicella*-like outline. The guard cells are longer than broad, but the frequent fusion of the delicate outer walls of the guard and accessory cells gives a false appearance of extreme breadth to the stomata. The development of the stomata seems to follow the *Litsea* plan, the segmentations which ultimately cut off the guard cells following the same kind of sequence as an apical cell. The number of ordinary epidermal cells surrounding the stomatal group is variable; it may be as many as five or as few as three. Twin stomata are frequent. The epidermal parenchyma is



TEXT-FIGS. 22, 23.—*Lindera rubronervia.*

very slightly sinuate or straight-walled. The venules bear deeply staining hair-bases from which sometimes unicellular acicular hairs project.

*Upper Epidermis.*—The parenchyma is regular and almost straight-walled.

LINDERA STRYCHNIFOLIA Villar

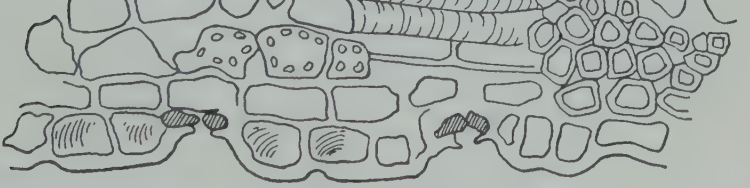
*Lower Epidermis* (Pl. **14**. fig. 64).—Scale-bearing guard cells are overarched by delicate subsidiary cells unequal in size; the outline of the pore is often like *Pseudonavicella*, especially when the accessory cells gape widely. From the scales of the guard cells tenuous cuticularized strands pass to the poles.

The parenchyma has sinuate walls and is crossed by a rectangular meshwork of venules, also with sinuate cells. On the venules, especially where they intersect, there are sclerenchymatous hair-bases, which in some cases bear long unicellular hairs.

*Upper Epidermis.*—Thick-walled sinuate parenchyma constitutes the upper epidermis. A very few hair-bases are to be seen at wide intervals.

LINDERA RUFA Gamble

*Lower Epidermis* (Pl. **14**. figs. 65, 66).—Depressed scale-bearing guard cells with prolonged and often nodulose terminations are overarched by paired unstained accessory cells, which may meet over the pore.



TEXT-FIG. 24.—*Lindera rufa.* Vertical section.

These cells are readily removed by maceration, and the guard cells are then exposed. Small thick-rimmed openings, single or paired, are abundant. They may possibly be hair-bases, but there is no evidence of hairs themselves, nor are the cells round these openings as definitely radiately grouped as is common with hair-bases.

The parenchyma is moderately thick with here and there a slight sinuation in a wall. The venules are thick-walled, and where three or four intersect become much wider.

*Upper Epidermis.*—This is entirely built up of thick straight-walled parenchyma.

*Vertical Section* (see text-fig. 24).—A vertical section through this leaf reveals the very tough cuticle and crenulated surface of the lower epidermis. The stomata are very deeply sunk and bear cuticular ridges projecting over them, while the cuticle dips deeply down to cover them. Adjacent cells overarch them and form accessory cells. The scales arise as cuticular outgrowths.

### *General Characters of the Cuticles of the Genus* Lindera.

The cuticle is thin-walled, sometimes hairy (*L. pulcherrima*) or glandular (*L. Prattii*). The stomata are somewhat variable in size and are often depressed and overlapped, or may be merely bordered by a pair of accessory cells, between which can be seen the guard cells, bearing on their upper surface cuticular ridges on very definite scales. The poles of the long axes of the guard cells and scales are prolonged and nodulose or distended, presenting a tumid appearance. These ends do not stain, and readily break down. The whole poral outline of the stoma resembles that of *Pseudonavicella.* The accessory cells are unequal in size, and one is sometimes triangular with its base parallel to the poral rim. They do not stain deeply and may remain quite unstained. Their junctions with the guard cells may break down, and then the stomata appear extremely broad. In those species in which the accessory cells overlap the guard cells, the former are commonly somewhat jaw-like in shape, much like the mandibles of the Crayfish, and only when these jaws are open can the guard cells be seen. In some species (*L. Oldhami*) a whole ring of accessory cells girdles the depressed guard cells. The lower epidermal parenchyma may be straight-walled (*L. Prattii* and *L. pulcherrima*) or sinuate (*L. præcox, L. strychnifolia*), and the cells may be papillate (*L. megaphylla, L. Meissneri*).

The upper epidermis consists of parenchyma which may be straight-walled (*L. Meissneri, L. Prattii*) or sinuate (*L. megaphylla, L. pulcherrima*).

The genus is distinguished from *Litsea* in its cuticular structures by the greater elongation of the scales and the terminally swollen prolongations of the guard cells.

### *b.* **Fossil Species.**

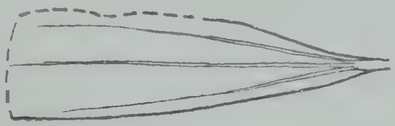
LINDERA CINNAMOMIFOLIA sp. nov.

*Occurrence.* Bournemouth Beds, Eocene.

*Locality.* Durley Chine. Several specimens have been found by the writer.

*External Characters* (Pl. **14.** fig. 67, text-fig. 25).—Leaf simple, lanceolate, entire; apex missing. The venation is characteristic: the midrib is well marked and from it two paired lateral veins pass upwards almost parallel to the margin. The angle made by both secondaries with the midrib varies from 7·5° to 8°. The blade passes gradually into the stalk. Length of blade present 4·5 cm., width 1 to 1·4 cm. Length of stalk 4 mm.

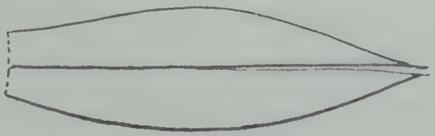
*Lower Epidermis* (Pl. **14**. figs. 68, 69).—Stomata are restricted to the lower surface. The guard cells are bounded by a pair of unequal accessory cells, one of which is often triangular with its base parallel to the stoma. These are distinguished from the remaining parenchyma by their differential staining, for whereas the ordinary epidermal cells stain deeply, the subsidiary cells hardly stain at all.



TEXT-FIG. 25.—*Lindera cinnamomifolia.*

The guard cells are somewhat longer than broad with colourless nodulose or tumid junctions, and bear a pair of upstanding scales which only rarely are partly closed, but usually stand open and erect. Often the delicate junctions of the guard cells, with their ridged scale continuations, are broken down. The epidermal cells are straight-walled, with occasionally a few triangular or round spaces which appear to be water pores. The meshwork of venules is rectangular, bearing now and again a rosette-like group of cells, some of which are very slightly papillate. In places these venules are accompanied by cavities running longitudinally which appear connected with the triangular pores.

*Upper Epidermis* (Pl. **14**. fig. 70).—This is entirely composed of straight-walled parenchyma, with a few pores similar to those of the lower epidermis. Delicate venules form a meshwork over the surface, and there are some ill-defined and small hair-bases.



TEXT-FIG. 26.—*Lindera cinnamomifolia* var. *porifera.*

LINDERA CINNAMOMIFOLIA var. PORIFERA var. nov.

*Occurrence.* Bournemouth Beds, Eocene.

*Locality.* Durley Chine, Bournemouth.

*External Characters* (text-fig. 26).—Leaf lanceolate, entire; apex missing. Midrib well marked, other veins not shown. Length 5·6 cm., width 2·6 cm.

*Lower Epidermis* (Pl. **14**. figs. 71, 72).—This is a slightly more xerophytic type than *L. cinnamomifolia.* There are fewer stomata (3 : 5 in the same area), which though varying in size are on the average somewhat smaller. The most distinctive feature is, however, the abundance of groups of small thick-rimmed triangular openings. These also occur in *L. cinnamomifolia*, but are nearly three times as numerous in the variety *porifera.*

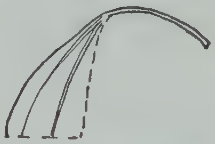
*Upper Epidermis.*—The triangular pores are again very numerous.

LINDERA BATHERI sp. nov.

*Occurrence.* Bournemouth Beds, Eocene.

*Locality.* Cliffs between Alum and Middle Chines.

*External Characters* (text-fig. 27).—Basal fragment of leaf alone preserved. A basal vein, evidently one of two, springs from the junction of stalk and blade at the side of the midrib and curves upwards parallel to the margin. Stalk slender, 1·7 cm. long.



TEXT-FIG. 27.—*Lindera Batheri.*

*Lower Epidermis* (Pl. **14**. figs. 73, 74).—Stomata are confined to the lower surface, which is more delicate than that of *L. cinnamomifolia.* The guard cells are not obviously depressed, but bear a pair of elongated narrow scales projecting over their upper surface, with a deeply staining rim towards the pore. The polar terminations of the scales and guard cells are unstained and sometimes tumid or nodulose. Rarely only can the polar prolongations of the scales be seen.

A pair of sometimes unequal cells, taking up stain very faintly or not at all, borders the guard cells parallel to their long axes. Four or five deeply staining epidermal cells encircle each stomatal group, which is of variable size. The epidermal cells differ from those of *L. cinnamomifolia* in being markedly sinuate, so that there is much resemblance to the recent *L. præcox*; the stomata, however, are larger in the fossil, and also the epidermal cells are smaller than in the recent species; hence the fossil is probably specifically distinct. There are no glandular openings, nor any indication of hairs.

*Upper Epidermis* (Pl. **14**. fig. 75).—This consists of sinuate parenchyma bearing numerous small pores similar to those seen in such abundance in *L. cinnamomifolia* var. *porifera.* The sinuations are less marked than in the lower epidermis.

*Summary.*—The fossil *Lindera* leaves described are characterized by the presence of paired secondary veins springing from the base of the midrib, so that the lower part of the leaf appears trinerved. This is a feature typical of many recent species of *Lindera* (*L. rubronervia*, *L. pulcherrima*, *L. strychnifolia*, *L. rufa*, *L. Prattii*). Fossil and recent forms agree also in the simple character of the leaves, their oblong-lanceolate or ovate shape, and their entire margin.

The cuticles of recent and fossil species exhibit the following characteristics in common :—Scale-rimmed guard cells whose axial terminations are somewhat prolonged, often nodulose, and staining faintly if at all. The general poral outline is much like that of the diatom *Pseudonavicella*. The guard cells are bordered by a pair of differentially staining accessory cells, unequal in size. They are usually rounded at right angles to the pore, rather than acutely triangularly distended as in *Neolitsea*.

In common with other members of the Lauraceæ, *Lindera* has the stomata restricted to the lower surface, and there is much variability of size in the stomatal groups. The guard cells bear scales or cuticular ridges on their upper surface, which are connected to the poles by cuticularizations. Accessory cells border the guard cells and may completely interlock over the pore (*L. pulcherrima*, *L. Prattii*, *L. rufa*). This is also seen in some species of *Litsea*, but the apical cell type of segmentation of the stomata is not as clearly evidenced in *Lindera* as in *Litsea* or *Neolitsea*.

The epidermal cells may be straight-walled (*L. Prattii*, *L. cinnamomifolia*) or sinuate (*L. præcox*, *L. Batheri*). The cuticle may be glandular (*L. Prattii*, *L. cinnamomifolia*). The fossil species described have strong cuticles with less stomatal protection by accessory cells or papillate cells, hairs, etc. than the recent forms.

## V. General Conclusions.

The minute details of plant anatomy revealed by the study of cuticular structure are seen to yield valuable data for interpretating certain floras of past geological times. The method is, however, limited to those plants which by virtue of their tough skin are capable of preservation in sedimentary deposits. In this respect the selection of the Lauraceæ for investigation was indicated owing to the resistant character of the majority of their leaves. In the Bournemouth Eocene they are among the most abundant fossils with cuticle preserved, where indeed many of the lanceolate leaves with pinnate venation, strong midrib, and well preserved cuticle are revealed on microscopic examination as members of this family.

This research and the previous work on the Fagaceæ prove the possibility of identifying fossils by a careful and detailed comparison of their cuticles with those of living genera.

Within the family Lauraceæ, the cuticular characters of the genera dealt with may be summarized as follows :—*Aniba* has a tough, resistant epidermis. The lower surface bears depressed guard cells with scales, bordered by two or four accessory cells, which in some species are markedly lobed and overarch the pore to which they impart a cruciform poral outline. The free edge of the accessory cells is strongly thickened in various species of this genus. Spicular ridges may be present in guard cells, accessory cells, and parenchyma. *Neolitsea* and *Litsea* are closely related genera with far less resistant cuticles than *Aniba*. They, too, have complex stomata. The guard cells bear scales or cuticular ridges and are bordered by unequal accessory cells, one of which may be more or less triangular. The wall common to accessory cell and guard cell tends to break down, giving an appearance of extreme breadth to the stomata. Differential staining is exhibited by these different cuticular elements.

*Lindera* has very thin-walled transparent stomata. The guard cells, which bear scales, are variable in size, often depressed, and are overlapped or bordered by a varying number of accessory cells. The poles of the long axes of the guard cells and scales are prolonged and nodulose ; these polar terminations do not stain, and often break down. The whole poral outline, where it is not hidden by projecting accessory cells, is like that of *Pseudonavicella*.

The cuticular structure in these genera and in others not described in detail in the present paper, indicates that the stomata of the Lauraceæ have a distinct family resemblance.

The present investigation demonstrates the presence of one species of *Aniba* and of various species of *Neolitsea*, *Litsea*, and *Lindera* in the Eocene of Bournemouth. It is interesting to note that the genera *Laurus* and *Cinnamomum*, which are very commonly described as leaf-impressions in Tertiary deposits, and which have quite distinctive cuticles, have not yet been recognized in the Bournemouth flora.

It is evident that the physiological characters of the fossil Lauraceous cuticles here described are such as at the present time are associated with the need for controlling transpiration. Such characters as the depressed stomata, the protection of the pore by scales, the formation of a vestibule by overarching accessory cells—the hairs, the thick cuticle—the spicules, will doubtless be of assistance in interpretation of the nature of the flora and the climate of Middle Eocene time in England.

I have to thank Dr. F. A. Bather, of the Geological Department of the British Museum, and Dr. A. B. Rendle, of the Botanical Department, for allowing me the use of these departments. I owe much gratitude to Mr. W. N. Edwards for his continuous helpful criticism. The cuticle photographs in the paper are the work of Mr. F. W. Edwards, those of external leaf-form by Mr. Herring, to both of whom I offer my hearty thanks.

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## EXPLANATION OF THE PLATES.

### PLATE 12.

*Aniba Gardneri.*

Fig. 1. Under epidermis, × 135.

Fig. 2. Under epidermis, × 540. Depressed scale-bearing guard cells and overlapping accessory cells whose free border is strongly cuticularized, and which vary in number. Note hair-base almost in the middle of the field.

Fig. 3. Under epidermis, × 30. Irregular dark cruciform stomatal areas. Straight-walled parenchyma. Meshwork of venules intersecting at wide angles. Cf. *A. spiculata* (fig. 21).

*Aniba firmula.*

Fig. 4. Under epidermis, × 135.

Fig. 5. Under epidermis, × 540. Stomata with guard cells covered by 1–3 lobed interlocking accessory cells.

Fig. 6. Under epidermis, × 30. Dark quadrangular stomatal areas often cruciform. Sinuate-walled parenchyma. Intersecting venules, which meet at wide angles, almost right angles. Cf. *A. spiculata* (fig. 21).

*Aniba lævigata.*

Fig. 7 Under epidermis, × 135.

Fig. 8. Under epidermis, × 540. Paired deeply-lobed unequal accessory cells, often bilobed with free thickened border, project over sunk scale bearing guard cells

*Aniba Ridleyana.*

Fig. 9. Under epidermis, × 135. Guard cells bearing large scales. Thick straight-walled parenchyma.

Fig. 10. Under epidermis, × 540. Guard cells covered with large scales, spicule-bordered.

*Aniba Hostmanniana.*

Fig. 11. Under epidermis, × 540.

Fig. 12. Under epidermis, × 540. Scale-rimmed guard cells bordered by four epidermal cells, sometimes bilobed.

*Aniba robusta.*

Fig. 13. Under epidermis, × 135. Guard cells covered by large scales. Thick straight-walled parenchyma. Thick venules dilated here and there, bearing hair-base.

Fig. 14. Under epidermis, × 540. Guard cells with scales, surrounded by epidermal cells of which opposite ones are often unequal in size.

*Aniba bracteata.*

Fig. 15. Under epidermis, × 135.

Fig. 16. Under epidermis, × 540. Scale-covered guard cells surrounded by two or four encircling lobed V-shaped accessory cells. Spicular outgrowths under and round some of the scales.

*Aniba amazonica.*

Fig. 17. Under epidermis, × 135.

Fig. 18. Under epidermis, × 540. Scale-covered guard cells encircled by four epidermal cells. Opposite girdling cells are unequal in size and sometimes V-shaped.

*Aniba desertorum.*

Fig. 19. Under epidermis, × 135. Much like *A. amazonica* but parenchyma is straight-walled.

Fig. 20. Under epidermis, × 540. Guard cells bearing open or closed scales, and bordered by four unequal accessory cells. Spicules present in some guard cells, bordering accessory cells and some epidermal cells; *cf.* the lowest hair-base on the right of the field, with spicules in the surrounding cells.

*Aniba spiculata.*

Fig. 21. Under epidermis, × 30. Dark, irregular, frequently cruciform stomatal areas. Straight-walled parenchyma. Intersecting venules, branching at wide angles, almost right angles.

Fig. 22. Under epidermis, × 540. Stomata, consisting of depressed scale-bordered guard cells surrounded and overlapped by bilobed accessory cells packed with spicules. Straight-walled pitted parenchyma with spicules in some of the cells.

Fig. 23. Under epidermis, × 540. Here the surrounding accessory cells do not all overlap the guard cells which are unusually abundant in this small portion of the preparation. The pore with scale-bearing guard cell can be seen.

Fig. 24. Under epidermis, × 90. Dark, deeply-lobed accessory cells surround a pore often cruciform; *cf.* with figs. 1, 4, 7. Straight-walled parenchyma.

## PLATE 13.

*Aniba spiculata.*

Fig. 25. External characters.

*Neolitsea apoensis*

Fig. 26. Under epidermis, × 540. Two stomatal groups each with one triangular accessory cell. Thickened poral rim bearing scaly ridges, between accessory cells. Thick-walled hair-base.

*Neolitsea formosa.*

Fig. 27. Under epidermis, × 540. Stomata with unequal accessory cells. Scale-bordered pores. Sinuate parenchyma.

Fig. 28. Under epidermis, × 135.

*Neolitsea triplinervia.*

Fig. 29. Under epidermis, × 540. Stomata showing horizontally elongated unequal triangular accessory cells.

Fig. 30. Under epidermis, × 135. Each stomatal complex irregular in outline, tending to be triangular. Sinuate parenchyma with thick-walled venule. Hair-bases.

*Neolitsea zeylanica.*

Fig. 31. Under epidermis, × 540. Guard cells with delicate triangular unequal accessory cells and pores rimmed by cuticular ridges. Slightly sinuate parenchyma. (*Cf.* lowest right stomatal complex with those of *N. Gardneri*, fig. 34.)

Fig. 32. Under epidermis, × 135.

*Neolitsea Gardneri.*

Fig. 33. External characters. V. 12650.

Fig. 34. Under epidermis, × 540. Scale-rimmed pores bordered by paired unequal accessory cells and each surrounded by four epidermal cells. Sinuate parenchyma.

Fig. 35. Under epidermis, × 135.

*Litsea Stocksii.*

Fig. 36. Under epidermis, × 540. Papillate epidermal cells surrounding stomata. Heavily cutinized jaw-like accessory cells bordering pores in which scales project.

Fig. 37. Under epidermis, × 135.

*Litsea fuscata.*

Fig. 38. Under epidermis, × 540. Scale-bordered guard cells heavily cutinized on their upper surface, here and there triangular in outline. Straight-walled parenchyma. Hair-bases.

Fig. 39. Upper epidermis, × 135.

*Litsea sebifera.*

Fig. 40. Upper epidermis, × 540. Guard cells and well-marked accessory cells. Thin-walled parenchyma. Strongly cutinized poral rim.

Fig. 41. Under epidermis, × 135. Stomata with accessory cells which here and there show a triangular character, girdled by four to five epidermal cells. Hair-bases.

*Litsea Edwardsi.*

Fig. 42. Under epidermis, × 540. Band. Coll. Cat. No. 307. Stomata consisting of guard cells with scales and accessory cells. Mode of segmentation of accessory cells seen well (see lowest left-hand stomatal complex). Thin-walled parenchyma with an occasional sinuation.

Fig. 42 *a*. One stoma, × 540, from another specimen of *L. Edwardsi.*

Fig. 43. Under epidermis, × 135. Band. Coll. Cat. No. 307. Cf. *L. sebifera* (fig. 41).

Fig. 44. Upper epidermis, × 135. Sinuate parenchyma with small venules and hair-bases.

Fig. 45. External characters of *L. Edwardsi.*

## PLATE 14.

*Litsea hirsuta.*

Fig. 46. External characters.

Fig. 47. Under epidermis, × 540. Stomata showing guard cells and confluent accessory cells. Polar junction of guard cells destroyed. Poral rim bearing scales or thickened ridges. Straight-walled parenchyma. Hair-base.

Fig. 48. Under epidermis, × 135. Stomata with confluent accessory cells, whose triangular outline shows well. Cf. *L. fuscata* (fig. 39).

*Litsea bournensis.*

Fig. 49. External characters.

Fig. 50. Under epidermis, × 540. Stomata unequal in size, showing serial segmentation of accessory cells. Guard cells with scale-rimmed pores and showing confluence with accessory cells.

Fig. 51. Under epidermis, × 135.

*Lindera megaphylla.*

Fig. 52. Under epidermis, × 540. One stomatal complex.

Fig. 53. Under epidermis, × 135.

*Lindera Oldhami.*

Fig. 54. Under epidermis, × 540. One stomatal group.

Fig. 55. Under epidermis, × 135. Groups of stomata. Thin-walled slightly sinuate parenchyma. Venules bearing hairs and hair-bases.

*Lindera Meissneri.*

Fig. 56. Under epidermis, × 540.

Fig. 57. Under epidermis, × 135. Stomata embedded in papillate parenchyma.

*Lindera pulcherrima.*

Fig. 58. Under epidermis, × 135.

*Lindera Prattii.*

Fig. 59. Under epidermis, × 540.

Fig. 60. Under epidermis, × 135. Stomata and parenchyma with venules.

*Lindera præcox.*

Fig. 61. Under epidermis, × 540. Guard cells with scales projecting from their backs. Bordering accessory cells unequal. Sinuate parenchyma.

*Lindera rubronervia.*

Fig. 62. Under epidermis, × 540. Three stomata. Thin-walled guard cells with accessory cells and deeply staining scales, in one case partly torn away.

Fig. 63. Under epidermis, × 135. Transparent stomata with deeply staining scales open and closed.

*Lindera strychnifolia.*

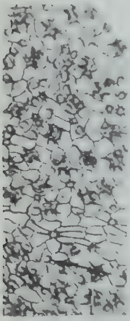
Fig. 64. Under epidermis, × 135. Stomata and parenchyma. Venules, with hairs and hair-bases.

*Lindera rufa.*

Fig. 65. Under epidermis, × 540

Fig. 66. Under epidermis × 135.

Bandulska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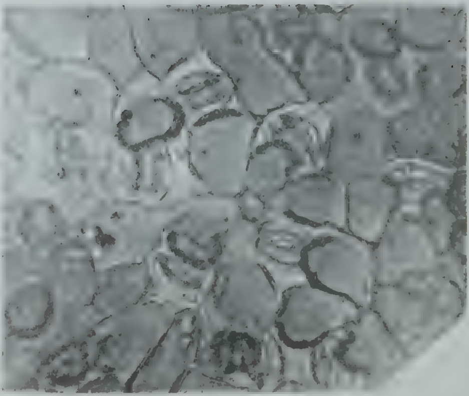
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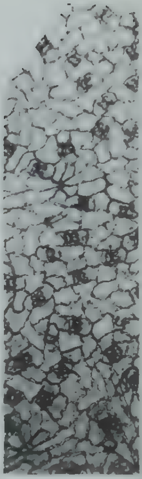
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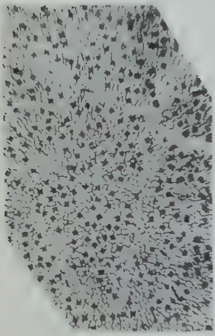
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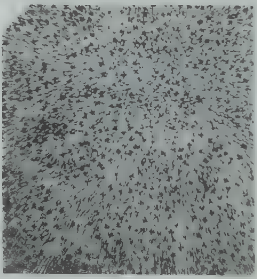
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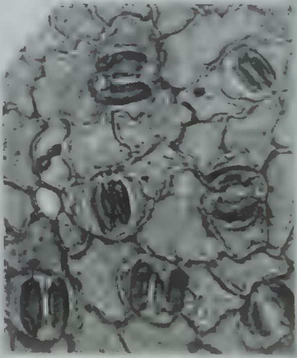
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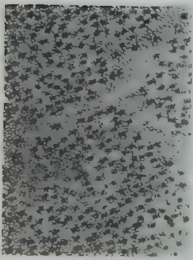
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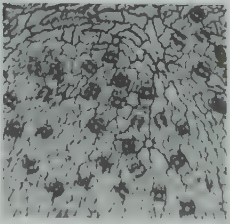
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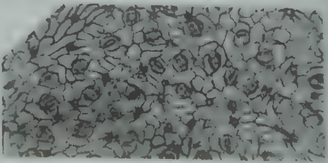
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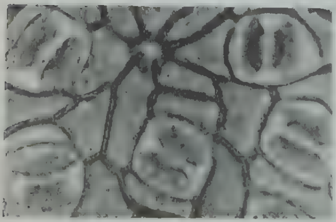
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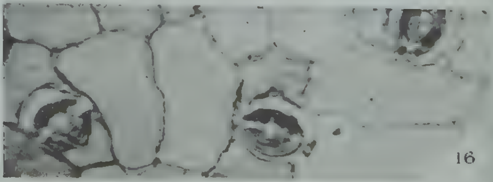
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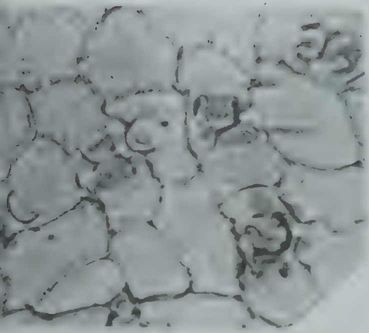

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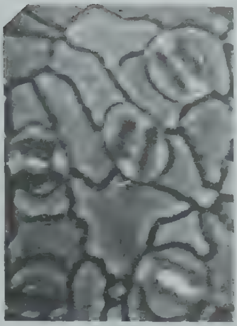

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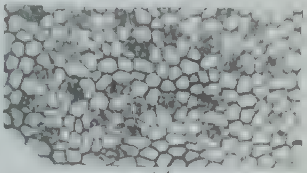

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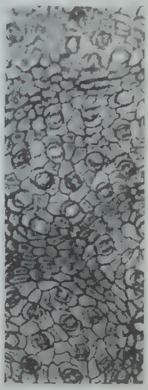

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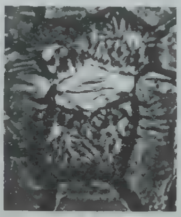

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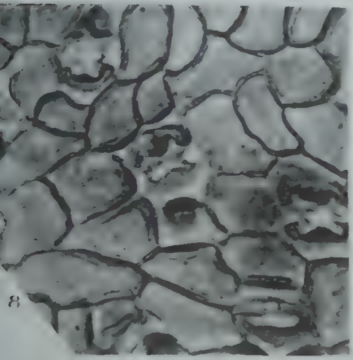

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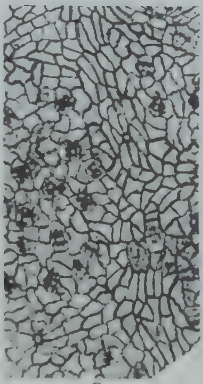

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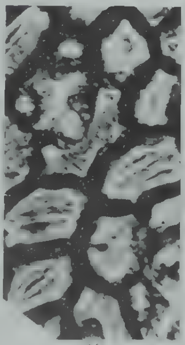

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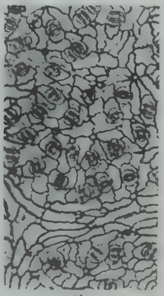

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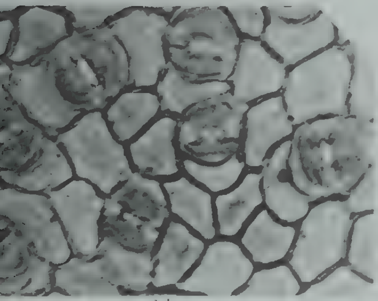

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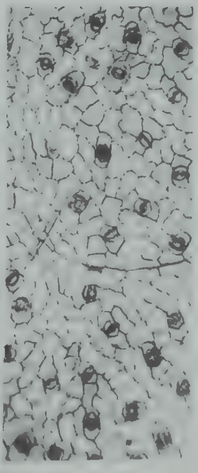

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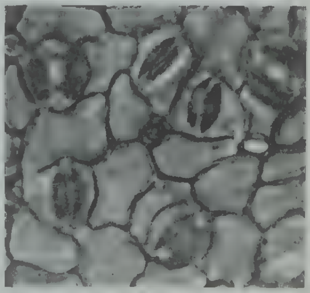

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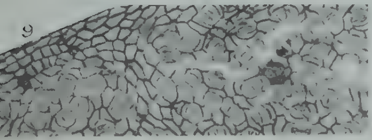

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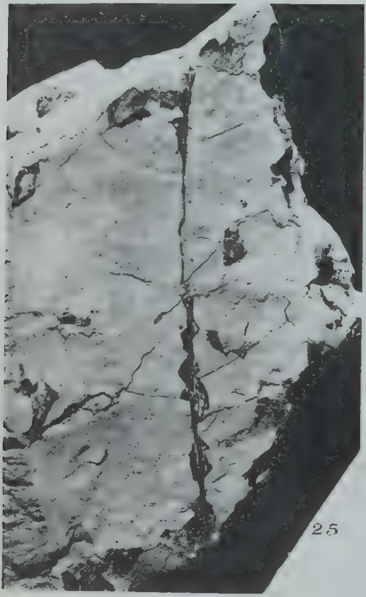
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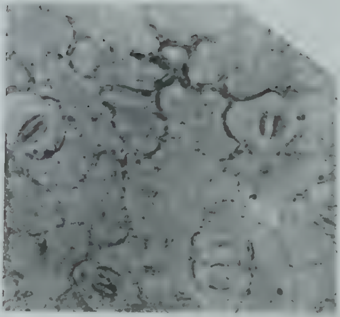
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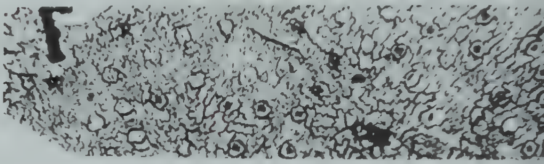
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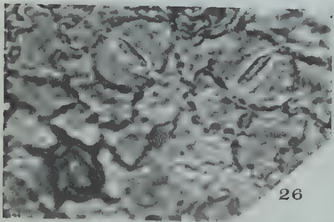
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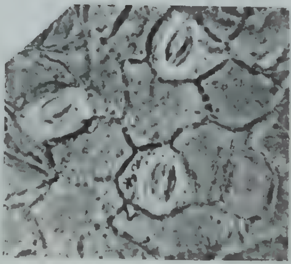
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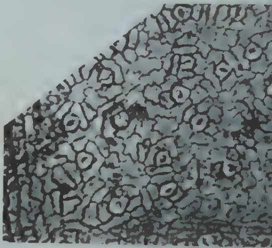
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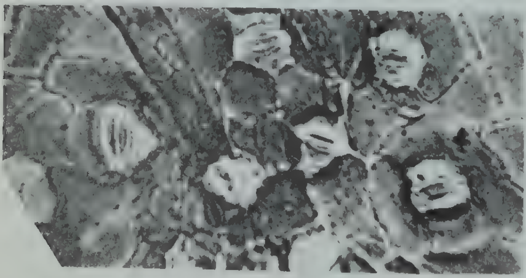
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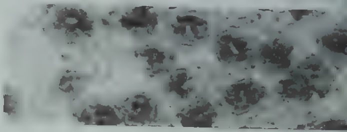
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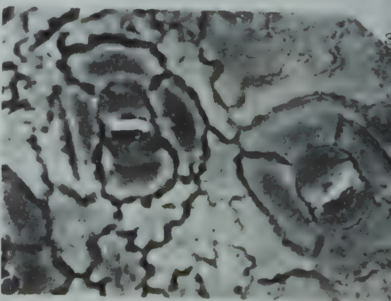

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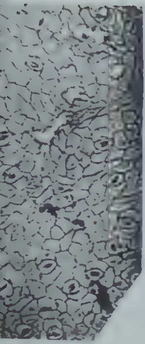
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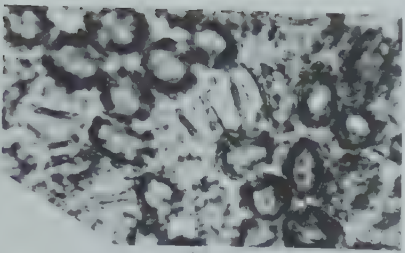
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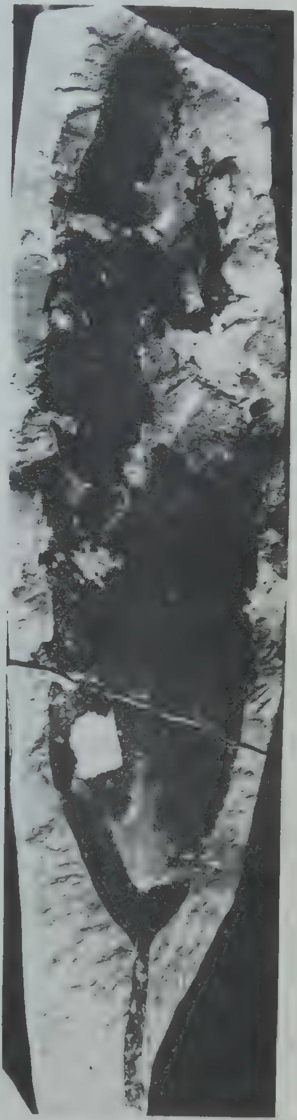
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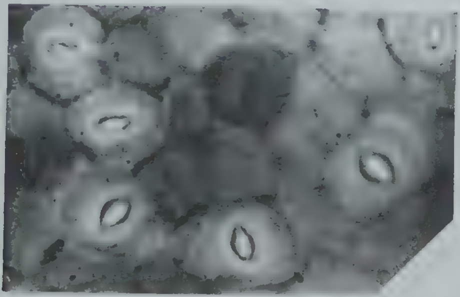
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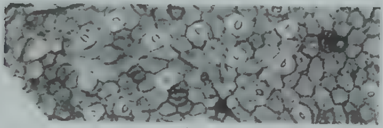
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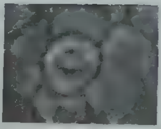
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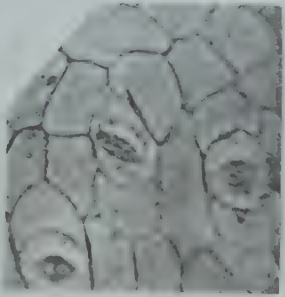
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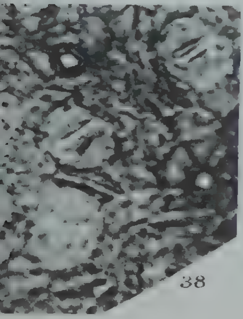
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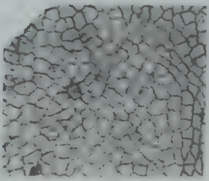
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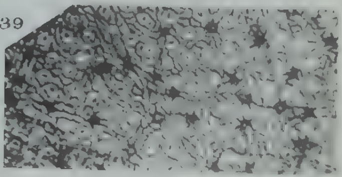
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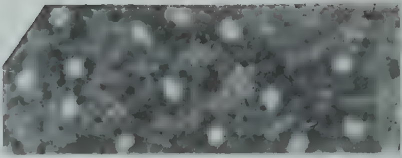

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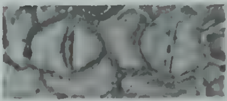

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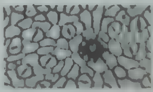

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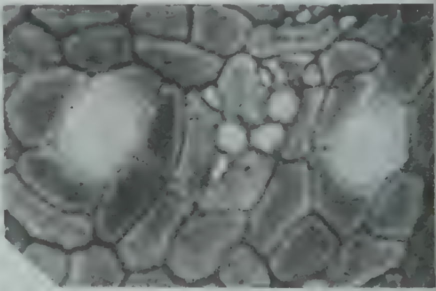

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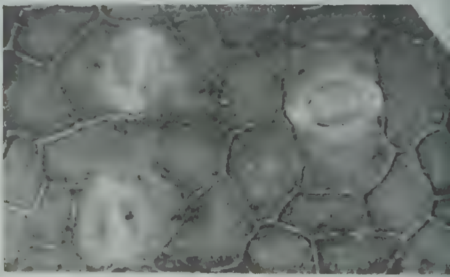

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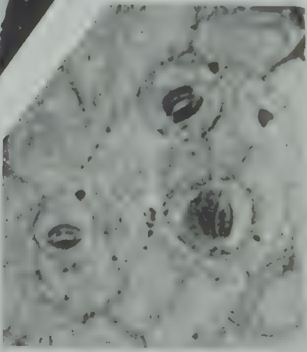

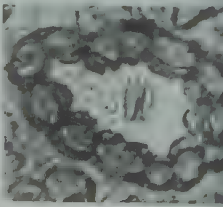

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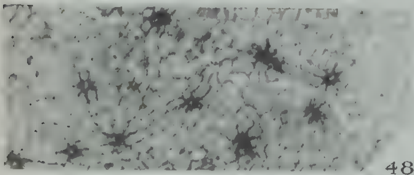

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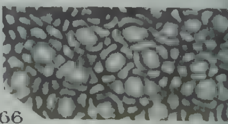

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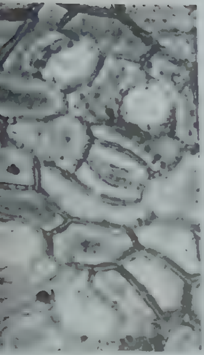

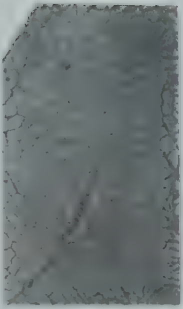

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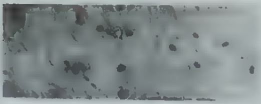

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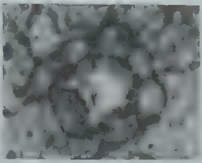

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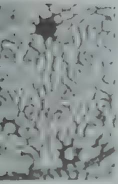

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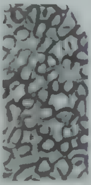

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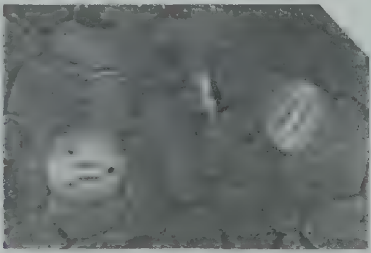

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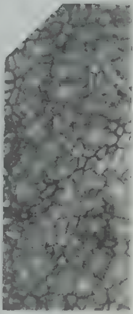

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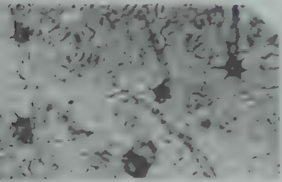

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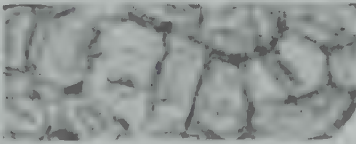

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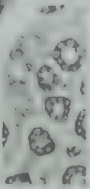

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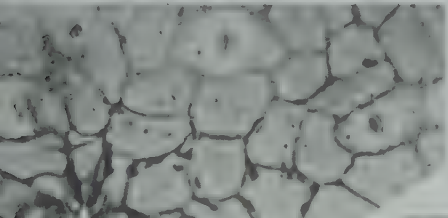

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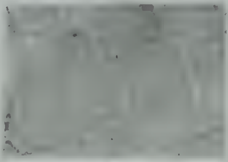

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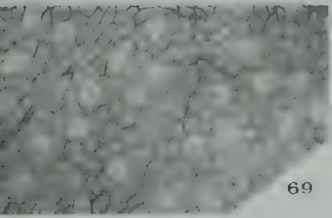

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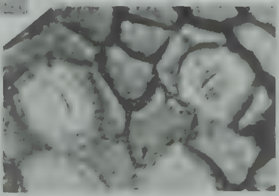

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*Lindera cinnamomifolia.*

Fig. 67. External characters. Cuticle is seen peeling from leaf.

Fig. 68. Under epidermis, × 540. Three stomata with accessory cells and nodulose terminations. The guard cells bear open scales and are like *Pseudonavicella.* Straight-walled epidermal cells.

Fig. 69. Under epidermis, × 135. Stomata with accessory cells. Guard cells with scales. Straight-walled parenchyma with water pores (?) and venules.

Fig. 70. Upper epidermis, × 135. Straight-walled parenchyma.

*Lindera cinnamomifolia* var. *porifera.*

Fig. 71. Under epidermis, × 540. Two stomata with parenchyma and "water pores.'

Fig. 72. Under epidermis, × 135. Stomata and straight-walled parenchyma. Very numerous groups of water pores.

*Lindera Batheri.*

Fig. 73. Under epidermis, × 540. Guard cells with scales and nodulose ends. Faintly staining accessory cells. Sinuate parenchyma.

Fig. 74. Under epidermis, × 135. Cuticle thin-walled. Stomata with parenchyma and venules.

Fig. 75. Upper epidermis, × 135. Sinuate parenchyma.

# Further Notes on the Genera *Fumaria* and *Rupicapnos*.

By H. W. PUGSLEY, B.A., F.L.S.

(PLATES 15–17.)

[Read 4th March, 1926.]

THE object of the present paper is to bring together such further information respecting these two genera as has accumulated since the publication of "A Revision of the Genera *Fumaria* and *Rupicapnos*," in vol. xliv. pp. 233 sq. (Botany) of the Journal of this Society (1919). At that time I was keenly alive to the disadvantage of dealing with the genus *Rupicapnos* without knowledge of any of its species in a living state, and so, when in the spring of 1923 an opportunity of visiting Algeria with Mr. E. G. Baker and Mr. Cecil Norman presented itself, I took advantage of the occasion to explore the habitats of these rare plants and was enabled, largely through the kindness of Drs. Battandier and Trabut, of Algiers, to collect representatives of three out of four of the generic sections. While in Algeria we saw also a large number of *Fumariæ*, and succeeded in adding two species to the flora of the country, one being a plant previously unknown and now described as *F. algeriensis*. More recently other material, largely the fruit of the latest botanical expeditions into Morocco, and providing further new forms both of *Fumaria* and *Rupicapnos*, has been received from Professor R. Maire of the University of Algiers, to whose kindness I am further indebted for the opportunity of seeing several important types, which previously I had been unable to examine. In addition to North African plants, a few other new forms from Britain, France, and Dalmatia are now described.

The figures in the third volume of the Cambridge British Flora, which, though written some years previously, was not published till 1920, are inserted as additions to the Icones cited in the Revision; and a few omissions in the text have been rectified and some emendations that suggested themselves carried into effect.

The sequence and general method followed in this paper are those of the Revision unless stated otherwise, and the new descriptions, with italicised principal contrasting characters, have been drawn up in the same manner.

## FUMARIA.

*Fumaria* Linn. (p. 250 of Revision).

l. 14. Add "Pugsley in Cambridge British Flora, iii. 171 (1920)."
l. 23. After "gibbum" insert "viridem."
l. 26. After "gibbum" insert "viridem."

Five new species of *Fumaria* appear in this paper, together with a number of new varieties. Two of these species, one from France and the other from Algeria, are possibly of hybrid origin, but they are very distinct and apparently fertile. *F. algeriensis* is an inconspicuous, small-flowered plant which is probably widely distributed in the interior of Algeria and Morocco. *F. maurorum* (already described by Dr. Maire) aud *F. ouezzanensis* are large-flowered species discovered in districts of Morocco recently occupied by the French.

Many of these North African Fumitories grow in natural habitats. In Morocco, where agriculture is in a primitive stage, they are commonly found on bare, uncultivated ground. *F. algeriensis* was first observed among the ruins of Timgad, and subsequently on a small outcrop of rock on Djebel Tougour, near Batna. Dr. Maire found *F. atlantica* in 1925 "in lapidosis calcareis mobilibus" in the Bou Taleb country. *F. rupestris* has repeatedly been recorded from calcareous rocks, and *F. macrosepala* and *F. ouezzanensis* occur in similar situations. Dr. Maire has found *F. Ballii* on schistose, rocky ground and *F. sepium* in bushy places and oak woods. *F. Vaillantii* var. *maroccana* and *F. Schrammii* var. *Pugsleyana* were also obtained from natural stations.

Specimens of *F. rupestris* received from Dr. Maire from the Zaer district of Morocco show the monstrous condition of the fruit already noticed in *F. muralis* at Madeira and *F. parviflora* in Spain (vide p. 253 of the Revision). This has been found due to a small fly, which apparently pierces the pericarp of the young fruit and deposits an egg therein, the larva feeding on the seed and pupating within the fruit. Affected fruits have been examined in the Natural History Museum and the insect identified as a species (at present undetermined) of the genus *Aylax* (*Cynipidæ*).

### SECTIO I. GRANDIFLORA.

To cover the anomalous species *F. mirabilis* the sectional diagnosis needs expansion as italicised, thus:—

Foliorum laciniæ . . . . . lanceolatæ (in *F. mirabili* . . . . . angustiores) . . . . . Flores . . . . . plus 9 mm. longi, *nisi in F. mirabili.*

### SUBSECTIO I. AGRARIÆ.

A slight emendation of the diagnosis of this Subsection, as italicised, may be made to cover the anomalous character of the outer petals in *F. rupestris* and the transfer of *F. flabellata* to the Subsection *Capreolatæ*, thus:—

Pedunculi breves aut *mediocres* . . . . . Petala exteriora . . . . . inferius marginibus (*sæpe in F. rupestre subobsoletis*) patentibus . . .

#### * Series **Eu-Agrariæ**.

1. FUMARIA AGRARIA Lagasca. (Pl. **15**. fig. 1 B.)

This curious plant (Lynes, Pl. Marocc. 1925, No. 26) recalling var. *elata* Ball was collected by Admiral Lynes at Bin-el-Ouidane, in the Middle Atlas of Morocco. The specimen shows finely cut foliage, a slender corolla as long as in typical *F. agraria* but with a larger spur, and fruits, so far as can be judged from immature examples, with a distinct apiculus marked with black. Unfortunately this plant cannot yet be precisely defined owing to the absence of developed fruit.

In addition to the habitats given in the Revision (p. 260) *F. agraria* occurs in Sardinia (Cagliari, Müller, in Hb. Kew!).

2. FUMARIA ATLANTICA Cosson & Durieu. (Pl. **15.** figs. 1 & 1 A.)

At Sidi Mecid and elsewhere about Constantine a plant was seen which is no doubt identical with that collected by E. G. Paris in 1869 (No. 205) and cited for this species in the Revision. The citation, taken from the sheet in Hb. Mus. Brit., which shows flowers but no fruit, as stated (*l. c.* p. 261), was inserted under the specific type. Another sheet of this set from Hb. Hauniense, however, which has been subsequently examined, possesses fruit agreeing with that of Reverchon's Kabylie material distinguished as var. *platyptera*, and as the essential difference between type and variety lies in the fruit in this case, Paris's exsiccata must be transferred to the variety.

My own gatherings around Constantine also agree in fruit characters with the original var. *platyptera*, although some of their fruits are larger, reaching 3 mm. in length and breadth. In this organ, which is distinctly less keeled than in typical *F. atlantica,* they closely approach the mucronulate-fruited forms of *F. major* Bad.

The flowers of this Constantine Fumitory are very pale pink, rather than white, in colour, and vary greatly in form. Above the Rummel gorge plants were noticed bearing moderate-sized corollas with the outer petals most broadly winged, like Reverchon's material that suggested the varietal name. At Sidi Mecid, on the other hand, there were much finer examples with corollas 15 mm. long, which were relatively narrowly winged—indeed more narrowly winged than in plants of *F. major* var. *algerica* that grew with them. But in spite of this variability, which extended to the leaf-cutting and length of pedicels and bracts, all the plants met with were evidently forms of the one variety *platyptera.* This variety, not only in its fruits but in its vigorous habit, long racemes (up to 30-flowered), and long pedicels, undoubtedly shows some affinity with *F. major* var. *algerica.*

Typical *F. atlantica* appears to be a rarer plant, which was not collected during my visit, and good flowering examples were not to be found in the herbaria of Dr. Battandier or the University of Algiers. When well grown, it seems to differ little from var. *platyptera* except in the form of its fruit, and the species as a whole is more closely related to *F. major* than to *F. agraria.*

*F. atlantica,* probably the variety *platyptera*, was also noticed by the railway near Constantine, and at one or two spots by the roadside between

Setif and Kerrata. A form of the variety, with deep pink flowers, occurred very sparingly at Milianah. The specific type has been collected recently (1925) by Dr. Maire in the Bou Taleb region of South Algeria.

3. FUMARIA OCCIDENTALIS Pugsley.

*Icon.* Insert "Cambridge British Flora, iii. pl. 180."

This species was collected by Miss E. S. Todd in 1922 at Mevagissey, Cornwall, considerably to the east of any previously recorded station.

4. FUMARIA RUPESTRIS Boissier & Reuter. (Pl. **15**. fig. 2.)

This species is very sparingly represented in British herbaria, and the original specimens in our collections received from Boissier are now fragmentary and in poor condition. The only Algerian examples at Kew that show flowers are those of Warion (including one from Tlemcen, the *locus classicus*) in which the corollas are distinctly smaller and narrower than in the Ronda plant collected by Bucknall and referred to at p. 262 of the Revision. Other Spanish material examined also has relatively large flowers. In the herbaria at Algiers there are several African gatherings of *F. rupestris*, all with flowers as in Warion's plants, and the species as seen growing at Milianah in 1922, in small quantity but good condition, also produced the same smaller, very narrow corollas. Dr. Maire has recently sent specimens gathered at Tlemcen in March 1923 whose corollas are identical except for a greater development of the wings of the outer petals, which might be expected in the earliest flowers.

It may thus be concluded that this narrow and rather small corolla is normal in *F. rupestris,* as seen in Africa, and this is indeed emphasized in Boissier's original description. His account of the Spanish plant, which he distinguished as var. *laxa*, mentions no floral difference, and was probably taken from a shade-form without good flowers. Haussknecht describes its flowers as smaller than in the type. It appears, however, from Bucknall's and other recent material that the Spanish form normally produces distinctly larger flowers than the African type, and it is therefore maintained as a variety under Boissier's name but with an amended description. It is possible that this larger-flowered plant occurs also in Africa, and it may be the variety *robusta* of Battandier & Trabut's Flora ; but a number of rampant, large-fruited African forms examined all show the typical small flowers.

A third distinct form, which has recently been discovered by Dr. Maire in Morocco, is described as var. *pallescens.*

The forms of this species should now stand as follows :—

*F. rupestris* Boiss. & Reut. Pugillus, 4 (1852).

*Exsicc.* Boissier & Reuter, Iter Alg.-hisp. 1849, Tlemcen, in Hb. Kew! Warion, Saida, 1872, in Hb. Kew! Warion, Pl. Atlant. Sel. 1878, No. 112, Tlemcen!

Fumaria *vix robusta*, satis ramosa, in arvis procumbens vel rarius petiolis cirrhosis scandens. Folia glaucescentia, foliolis in lobos lanceolatos oblongosve plus minusve acutos valde mucronatos fissis, irregulariter 2–3-pinnatisecta. *Racemi laxi*, sub-20-(sæpius 8–12-)flori, *pedunculos* breviusculos *superantes*. *Bracteæ* lineari-lanceolatæ, angustæ, setaceo-acuminatæ, *pedicellos* fructiferos apice incrassatos *suberectos fere æquantes*. *Sepala* 3–4·5 *mm. longa*, 1–2 *mm. lata*, *lanceolata* vel anguste oblonga, peltata, acuminata, *subintegra* vel paulo dentata, nervo dorsali lato viridiusculo valde carinata, albida, corollæ tubo angusto æquilata, in fructu diu persistentia. *Corolla angustissima*, 10–12 *mm. longa*, *pallide rosea*; *petalo superiore subacuto*, calcare longiusculo deflexo et *alis purpureis* apicem vix attingentibus carinamque raro æquantibus (interdum obsoletis) prædito; *petalo inferiore* angustissimo acuto *marginibus vulgo subobsoletis* raro angustis patentibus; petalis interioribus apice sursum curvatis atropurpureis. *Fructûs mediocres*, circa 2·5 mm. longi et 2 mm. lati, *subrotundo-ovati*, *obscure rostrati subapiculati*, plane carinati et paulo compressi, inferne multo angustati, nonnunquam apice minute nigro-maculati, siccitate apicis foveolis latis obscuris *dense* sed haud grosse *tuberculato-rugosi*.

β. *laxa* Boiss. & Reut. *l. c.* 5 (descriptio emendata); *F. arundana* Boiss. ap. Wilkomm & Lange, Fl. Hisp. iii. 880 (1880); *F. rupestris β. robusta* Batt. et Trabut, Fl. Alger. 27 (1880)?

*Exsicc.* Lange, Fl. Hisp. 1851–2, Jaen, in Hb. Haun., ut *F. flabellata*! Winkler, No. 504, Jaen, 1876, in Hb. Haun.! Reverchon, Pl. de l'Andalousie, 1890, No. 569, Ronda, ut *F. agraria*!

Robustior et laxior, interdum scandens. Racemi longiusculi. Sepala 3·5–5·5 mm. longa. *Corolla major*, *minus angustata*, 10–14 *mm. longa*, nonnunquam roseo-albida; petali superioris alis nunc purpureis carinam æquantibus nunc roseis angustioribus; *petali inferioris marginibus* nunc latiusculis patulis *subspathulatis* nunc angustissimis erectis. Fructûs majusculi, 2·5–2·75 mm. longi et 2·5 mm. lati, quam typi latiores. Aliter ut in typo.

γ. *pallescens* var. nov.

*Exsicc.* Maire, Lalla-Zitouna, prope Meknes, 1923, in Hb. Alger.!

Bracteæ pedicellis fructiferis plane breviores. *Sepala* quam in typo *minora*, 2–3 *mm. longa*. *Corolla apicem versus valde angustata*, 11–12 mm. longa, *albida*; petalo superiore acuto, calcare magno deflexo alisque subobsoletis prædito; petalo inferiore marginibus subobsoletis acuto; petalis interioribus apice breviter atropurpureis. Aliter verisimiliter ut in typo.

Hæc varietas distincta ad Lallam-Zitounam et ad Djebel Zalagh prope Meknes in imperio Maroccano crescit ubi a cl. Dr. Maire collecta est.

*F. rupestris* is widely distributed in Algeria north of the Hauts Plateaux and as far east as the Djurdjura. It has also been collected by Dr. Maire in various stations stretching across Morocco to the Cherrat valley in the Zaer district.

The very narrow, almost wingless corollas commonly seen in *F. rupestris* are so different from the flowers of the other members of the Subsection *Agrariæ* that its retention in that group seems at first sight very questionable. But it is clear from Dr. Maire's Tlemcen specimens, which show the earliest flowers, that the lower petal of well-developed corollas produces spreading margins as in the other Agrarian species, and fairly developed wings and margins also frequently appear in the Spanish form, indicating the same alliance. There is thus no real ground for removing *F. rupestris* from the Subsection *Agrariæ.*

4 *a.* FUMARIA MIRABILIS sp. nov. (Pl. **15**. fig. 3.)

*Exsicc.* Joly, Maison Carrée, 1897, in Hb. Alger., ut *F.* —— !

Fumaria habitu verisimiliter satis laxo. *Folia 3–4-pinnatisecta*, ut videtur viridia, foliolis in *lacinias* confertas planas *lineari-oblongas* acutas vel mucronatas fissis prædita. *Racemi* (etiam fructiferi) *densi*, 10–15-*flori, subsessiles* folio opposito conspicue breviores. *Bracteæ* lineari-oblongæ, integræ, breviter acuminatæ, *pedicellos* fructiferos *erecto patentes* brevissimos (circa 2 mm. longos) crassos *subduplo superantes. Sepala* 3–4 *mm. longa*, 1–1·5 *mm. lata, lanceolata*, acuta, *subintegra* vel parce denticulata, nervo lato rubicundo rosea, sæpe in fructu persistentia. *Corolla angusta*, 7–9 *mm. longa, rosea* ; *petalo superiore alis roseis* sursum reflexis carinam subæquantibus apicemque attingentibus *subacuto,* calcare verisimiliter breviusculo ; *petalo inferiore marginibus latiusculis patulis* apicem vix attingentibus *subacuto haud spathulato* ; petalis interioribus fere rectis apice atropurpureis. *Fructûs modici,* circa 2 mm. longi ac lati, *subrotundi*, paulo compressi et plane carinati, *obtusi submucronulati*, siccitate apicis foveolis obscuris tenuiter *tuberculato-rugosi.*

*F. mirabilis* apud Maison Carrée prope oppidum Algiers inventa est.

Hæc *Fumaria* notabilis, quæ per folia decomposita et per racemos subsessiles bracteis magnis præditos *F. micranthæ* faciem monstrat, Subsectionis *Agrariarum* corollam (quamvis minorem) et *F. rupestris* sepala longa habet. Forsitan inter *F. rupestrem* et *F. micrantham* hybrida sit, sed fructûs perfectos parit—id quod in hujus generis hybridis raro accidit. Planta igitur ut Subsectionis *Agrariarum* species abnormalis *F. rupestri* affinis depingitur.

This remarkable Fumitory was noticed, unnamed, in the herbarium of the University of Algiers and has now been described from material supplied through the kindness of Dr. Maire. As it was collected within easy distance of the town of Algiers, it may be expected to be refound, unless it is of hybrid origin and not permanently fertile. Its intermediate characters render its position in the genus doubtful, and it is possible that its true place is among the *Latisepalæ* near *F. micrantha.*

5. FUMARIA BALLII Pugsley.

This rare species has been rediscovered in Morocco. There is now a specimen at Kew labelled " C. J. Pitard, Mission au Maroc. No. 2904, Bir

Ydour, in arvis. May, 1913." Last year (1925) Dr. Maire also found it at Amismiz and Goundafa, in the Great Atlas, not very far from its original station.

6. FUMARIA MAJOR Badarro.

*β. spectabilis* Rouy.

This plant was seen in May, 1925, at Palavas, near Montpellier, as a shortly branched, open-ground plant, and at Carcassone, outside the ancient Cité, as an elongate, semi-shade form on banks and hedges. In both districts its racemes were clearly more floriferous than in typical *F. major*, frequently bearing as many as twenty-five flowers, which were uniformly of a paler colour. At Carcassone the fruits were markedly apiculate.

*γ. algerica* Pugsley. (Pl. **15**. fig. 4.)

This handsome Fumitory was observed in several localities in Algeria and was seen in remarkable luxuriance and beauty on the steep slopes immediately below the walls of Milianah, where it grew in such abundance that its crimson flowers coloured the whole hillside. It is notable, when vigorous, not only for its very long and floriferous racemes of large and brilliant flowers, but for its strong and remarkably erect habit. As already remarked, it resembles in several respects *F. atlantica* Coss. & Dur.

A few individual plants, hybrids between this variety and *F. capreolata*, which in places grew with it, were noticed at Milianah. They were of two forms: one of luxuriant and rampant growth, with very long, lax racemes of large flowers intermediate between those of the two species, and differing but little from the examples sent out by Verguin from the south of France as × *F. Burnati*: the second, with much denser but equally floriferous racemes of smaller flowers, somewhat resembling those of *F. Munbyi* Boiss. These hybrids produced a few developed fruits, but no perfect seeds were found.

7. FUMARIA GAILLARDOTII Boissier. (Pl. **15**. fig. 5.)

This species, not previously recorded from Algeria, was discovered at Mustapha Supérieur, above Algiers, and subsequently seen in greater quantity on the cultivated slopes above Milianah. Several Algerian examples under other names were also observed in the herbaria at Algiers, and a more recent specimen has been sent by M. d'Alleizette from the neighbourhood of Oran. The plant is evidently widely distributed in Algeria, and is perhaps the *F. Boræi* of Battandier & Trabut's Flora.

There are specimens of *F. Gaillardotii* from South Italy (Naples) in Hb. Haun., and from Malta in Hb. Mus. Brit., in addition to the localities given in the Revision.

*F. Gaillardotii* when growing cannot easily be mistaken for *F. major* owing to its usually decumbent or almost prostrate habit, and its much shorter racemes of smaller and lighter flowers.

### ** Series **Orientales.**

8. FUMARIA FLABELLATA Gasparrini.

This species is transferred to the Subsection *Capreolatæ* (No. 13 *a*), q. v.

9. FUMARIA JUDAICA Boissier.

In 1921 a number of specimens of *F. judaica*, mostly from the smaller Dalmatian islands, were received for examination from Dr. Ginzberger, of Vienna, and more recently further Egyptian material has been seen in Hb. Haun.

From this material a fresh description of the typical species has been drawn up, thus :—

*F. judaica* Boiss. Diag. Pl. Or. ii. No. 8, p. 15 (1849).

Fumaria *satis robusta*, plus minusve ramosa, suberecta diffusa vel petiolis cirrhosis scandens. Folia irregulariter 2–3-pinnatisecta, foliolis in lobos lanceolatos acutos vel oblongos mucronatos fissis prædita. *Racemi* 10–20-flori, *laxiusculi, pedunculos* sæpius *paulo superantes. Bracteæ* lineari-lanceolatæ, tenuiter acuminatæ, *pedicellis* fructiferis longitudinis variabilis apice vulgo valde incrassatis *suberectis dimidio* vel parte tertiâ *breviores. Sepala parva, circa 2 mm. longa*, 1 *mm. lata, oblongo-lanceolata*, acuminata, vix peltata, basin versus *plus minusve dentata*, nervo viridiusculo albida. *Corolla* 9–11 *mm. longa*, primo *albida* tandem sæpe roseo-tincta ; *petalo superiore alis albidis* reflexis carinam superantibus apicem attingentibus et calcar adscendens versus longe productis *obtuso*; *petalo inferiore marginibus latiusculis patentibus* albidis apicem fere attingentibus obtusiusculo ; *petalis interioribus* sursum curvatis *apice breviuscule atropurpureis. Fructûs magni*, circa 3 mm. longi ac lati, *subrotundi*, superne *obtusissimi* vel etiam leviter retusi (juniores mucronulati), carinâ mediocri sed paululum compressi, siccitate apicis foveolis obscuris sæpe nigro-maculatis plus minusve nitidi *valde* (præsertim ad foveolam interiorem) *tuberculato-rugosi.*

The majority of Egyptian examples of *F. judaica* show denser racemes and shorter pedicels than in the Syrian plants, but this difference is not constant, for some of the Alexandrian material in Hb. Haun. exactly matches Bornmüller's Jaffa gathering No. 46.

The range of *F. judaica* extends from Syria and Egypt westwards along the south coast of Asia Minor to the Greek Islands and the Adriatic. It is recorded for Lycia by Haussknecht, and there is a Cyprus specimen at Kew and one from Crete in Hb. Haun. It is also given for the Ægean Islands in Vierhapper's recent 'Flora Griechenlands' (1914). In 1911 it was found by Dr. Ginzberger in some of the rocky Dalmatian islets, where it seems certainly native; and as it occurs both in Lesina and Pelagosa, Haussknecht's record for Monte Gargano in South Italy might be expected. The variety *insignis* was also found by Dr. Ginzberger in the Dalmatian Islands Bacili and Veli Barjak.

### SUBSECTIO II. CAPREOLATÆ.

A slight amendment of the description of the lower petal in the subsectional diagnosis is necessitated by the transfer of *F. flabellata* from the *Agrariæ*. This should read ". . . . petalo inferiore acuto marginibus apicem haud attingentibus *sæpius* erectis angustis *raro patulis plus minusve latis*."

#### * Series **Eu-Capreolatæ**.

The fruit of this series should now be "læves ad *tuberculato-rugosi*."

12. FUMARIA CAPREOLATA Linn.

This species is very common around Algiers, both on cultivated ground and on hedgebanks. It was likewise noticed in similar situations about Blidah and Milianah. At Algiers and at Ain-Taya, on the coast, the variety *speciosa* Hamm. also occurred, apparently keeping quite distinct from the type and often bearing flowers of the most vivid crimson.

γ. *albiflora* Hamm.

A well marked form of this variety was collected in 1919 by Admiral Lynes at Azrou, in the Middle Atlas of Morocco.

ε. *devoniensis* Pugsley.

Insert "*Icon.* Cambridge British Flora, iii. pl. 181."
and "*Exsicc.* Pugsley, No. 73 !"

The variety *Hochreutineri* is further dealt with under *F. dubia*.

At Algiers the opportunity was taken to examine Pomel's original material of his *F. platycalyx* from Tiaret. This is no longer in good condition, but while showing the essential characters of *F. capreolata*, it seems distinguishable by its very large sepals and rotund fruits. Pomel's description includes these distinctive features, and his critical judgment in this family cannot be lightly set aside. This plant, which was found in an apparently natural habitat (shady spots at the foot of rocks), is therefore now treated as an additional variety of *F. capreolata*, thus:—

θ. *platycalyx* var. nov. *F. platycalyx* Pomel, Nouv. Mat. Fl. Atlant. 239 (1874).

*Exsicc.* Pomel, Tiaret, 1860, in Hb. Alger., ut *F. platycalyx* !

*Sepala* relative *magna*, circa 6 mm. longa et 3 mm. lata, valde carinata. Corolla quam in typo minor, 10 mm. longa, albida, plus minusve roseotincta. *Fructûs mediocres*, circa 2·5 mm. longi ac lati, *fere orbiculares*, ad mediam latissimi. Aliter ut in typo.

Under the arrangement of the Revision this new variety should follow ε. *devoniensis*.

13. FUMARIA DUBIA Pugsley. (Pl. **15**. fig. 6.)

In the Revision (p. 272) this species is described from a solitary specimen in Hb. Boissier, collected near Algiers by Fauché in 1831. In 1922 a precisely similar plant was found above Mustapha Supérieur, where it was growing in fair quantity. While resembling *F. capreolata* in general *facies*, it differed obviously in its much smaller sepals, in the wings of the upper petal not being dark purple but white or rosy-pink like the rest of the corolla, and in the different shape of its fruit.

At El Biar and in the Frais Vallon, near Algiers, another Fumitory was met with which resembled Fauché's plant but bore dark-tipped flowers. This form, as observed, was remarkably floriferous, and from its dark-tipped flowers at first sight looked distinct.

A comparison of the material gathered in the three localities, however, showed that it all belonged to one species, which seems normally to bear dense racemes of dark-tipped flowers, but in certain conditions tends to produce shorter racemes and to lose the deep purple colour of the wings of the upper petal without any further depauperation, and even while a general rosy suffusion may persist. This variation, which does not appear to be that of an ordinary shade-form, is unusual in the genus and not easily explained, but it is probably an unstable one that would not necessarily be perpetuated by seed. The plant with dark-tipped corollas is therefore regarded as the normal state of the species and the pale-flowered one found by Fauché differentiated simply as a form.

The plant collected at Algiers by Dr. Hochreutiner and placed under *F. capreolata* in the Revision as var. *Hochreutineri* (of which no good fruit was seen) is now found to be a form of the typical *F. dubia* with dark-tipped flowers, and the varietal name under *F. capreolata* must be abandoned.

There is a small example of *F. dubia* in Hb. Mus. Brit. collected by Gandoger at Algiers as *F. flabellata*, and another from the Frais Vallon in Hb. Haun. forming part of a sheet of *F. capreolata*.

Mr. C. Norman has now placed an adequate specimen collected at Algiers in 1922 in Hb. Mus. Brit.

A revised description of *F. dubia* from the more adequate material now available is appended:—

*F. dubia* Pugsley, Revis. Fum. & Rupicapnos, 272 (1919).

Fumaria *vix robusta,* satis ramosa, sæpius petiolis cirrhosis scandens. Folia subglaucescentia, irregulariter 2–3-pinnatisecta, foliolis in lobos oblongos vel cuneatos (quam in *F. capreolatâ* paulo angustiores) plus minusve mucronatos fissis prædita. *Racemi densiusculi, multiflori* (15–30-flori), *pedunculos* satis graciles rectos *subæquantes* (sub-20-flori, longius pedunculati in formâ *Fauchëi). Bracteæ* angustæ, lineari-lanceolatæ, acuminatæ, *pedicellis* fructiferis 5–6 mm. longis gracilibus apice incrassatis *arcuato-recurvis tertiâ parte breviores. Sepala* 3·5–4 *mm. longa, circa* 2 *mm. lata, ovalia* vel lanceolata, peltata, acuminata, basin versus *denticulata,* nervo dorsali lato viridiusculo albida. *Corolla* 10–14 *mm. longa, angusta, fere recta,* *albida* vel tandem *pallide roseo-tincta*, rarius rubescens; *petalo superiore acuto*, calcare angusto parum curvato paululum deflexo et *alis atropurpureis* (roseis in formâ *Fauchëi*, nonnunquam albidis in formis umbrosis) reflexis apicem haud attingentibus carinamque haud æquantibus prædito; *petalo inferiore marginibus* angustissimis *suberectis vel* in flore bene explicato latiusculis *patulis* sed apicem nunquam attingentibus acuto; petalis interioribus parum curvatis apice breviter atropurpureis. *Fructûs modici*, 2·25–2·5 mm. longi, circa 2 mm. lati, *obovati* vel ovales, superne *in apicem subacutum* vel fere obtusum et inferne in stipitem quam pedicelli apex angustiorem *angustati*, paulo compressi sed obscure carinati, siccitate apice foveolis parvis distinctis plus minusve *rugulosi*.

*F. dubia*, which grows in several localities in the vicinity of Algiers, and probably extends over a wider area, differs from *F. capreolata* in its narrower leaf-segments, in its smaller, denticulate sepals, in the form of its less brightly tinted corolla, which has a slenderer and deflexed rather than ascending spur, and in its narrow, more or less subacute, rugulose fruits. It also shows some affinity with *F. flabellata* as observed by Haussknecht, especially in its liability to lose the usual dark purple colouring of the wings of the upper petal, which does not similarly affect *F. capreolata*. But *F. flabellata* differs greatly in its broader leaf-segments, broader and more broadly winged corollas, and much larger, more rugose and almost truncate fruits. Very large sepals, broad purplish corollas, and broad truncate fruits render *F. purpurea* also abundantly distinct. The *F. speciosa* referred to on page 27 of Battandier and Trabut's 'Flore de l'Algérie' appears to be *F. dubia*.

### 13 *a*. Fumaria flabellata Gasparrini.

After seeing this beautiful species growing in several stations around Bougie and *F. dubia* in considerable quantity near Algiers, the writer is convinced that the two plants cannot be placed in different subsections of the genus, and that their closest affinity is with *F. capreolata*. *F. flabellata* is therefore removed from the *Agrariæ* and placed in sequence to follow *F. dubia*. The normal corolla of *F. flabellata* is relatively of Agrarian form, being broad towards the apex and with a less developed spur than in *F. capreolata*, while the margins of the lower petal are clearly patent. But the upper petal, though broad, is apically acute as in the other *Capreolatæ*, and the margins of the lower petal are always narrowed towards the acute apex and not dilated there as in the true *Agrariæ*.

The fruit of *F. flabellata* is tubercular-rugose as in the *Agrariæ*, but in shape it recalls *F. capreolata*, and when fresh it shows the distinct, fleshy neck narrower than the dilated tip of the pedicel, which is a marked *Capreolatæ* feature. Its habit and inflorescence are clearly those of *F. capreolata*, but its white corollas seem less subject than in that species to the reddish dorsal suffusion after fertilisation.

*F. flabellata* varies remarkably in the development of its flowers. In plants growing under adverse conditions, the corolla sometimes remains quite narrow with the wings obsolete, or sometimes it may be more normal in shape but show no purple colour in the wings of the upper petal. Such plants look remarkably different from well-grown individuals and may sometimes resemble forms of *F. dubia*, but they can be at once distinguished by their larger, obtuse and rugose fruits.

Among the plants received for examination from Dr. Ginzberger in 1921 is a curious form from the Pelagosa Islands, sent as *F. flabellata*, which was at first thought to be a new species. The flowers in the material seen are unfortunately poor and ill-dried, and certainly not normal, but acquaintance with the living plant in Algeria proves that Dr. Ginzberger's name is correct. The uniformly straight pedicels, however, and the obovate fruits are so peculiar that the plant seems to merit distinction as a variety.

*F. flabellata* may be diagnosed thus :—

*F. flabellata* Gasp. in Rendic. Accad. Scien. Napoli, i. 51 (1842).

Fumaria *satis robusta* et ramosa, sæpe internodis longis elongata petiolisque cirrhosis scandens. Folia irregulariter 2–3-pinnatisecta, foliolis in lobos ellipticos cuneiformes vel oblongos, obtusos mucronatos vel subacutos fissis, infimis vulgo breviter petiolatis prædita. *Racemi* primo densi, tandem elongati, *multi-* (10–30-) *flori, pedunculos* plus minusve longos primarii *vix æquantes* superiores sæpe superantes. *Bracteæ* albidæ, lineari-lanceolatæ, acuminatæ, *pedicellis* fructiferis apice valde incrassatis *arcuato-recurvis* (in formâ umbrosâ rectis patulis) *paulo breviores. Sepala* 3–5 *mm. longa*, 1·5–2·5 *mm. lata, ovalia* vel ovata, peltata, acuminata, *basin* sæpe subtruncatam *versus dentata,* nervo dorsali viridiusculo albida. *Corolla magna,* 12–14 *mm. longa, alba*, nonnunquam dorso roseo-tincta ; *petalo superiore acuto, lato*, dorsum compresso, *alis* intense *atropurpureis* reflexis apicem vix attingentibus sed carinam superantibus (in formâ umbrosâ angusto, alis obsoletis vel albidis carinam haud æquantibus) prædito ; calcare quam in *F. capreolatâ* relative minore ; *petalo inferiore marginibus patulis* plus minusve latis apicem haud attingentibus acuto ; petalis interioribus apice sursum curvatis atropurpureis. *Fructûs majusculi*, 2·5–2·75 mm. longi ac lati, *subrotundo-quadrati, obtusissimi* et minute subretusi, satis carinato-compressi, in vivo inferne in stipitem distinctum quam pedicelli apex incrassatus plane angustiorem contracti, siccitate apicis foveolis distinctis *dense tuberculato-rugosi* et sæpe uno latere nigro-maculati.

*β. adriatica* var. nov.

*Exsicc.* Ginzberger, Pelagosa grande, 2 Mai, 1895, in Hb. Vindob., partim, ut *F. flabellata* !

Racemi 12–20-flori, laxiusculi ; bracteæ *pedicellis fructiferis rectis* subpatentibus deflexisve dimidio breviores, vel infimæ paulo longiores. Sepala circa 3·5 mm. longa, 2 mm. lata, ovata. *Corolla* 10–12 *mm. longa, angusta,* verisimiliter albida ; petalo superiore acuto alis purpureis carinam subæquantibus. *Fructûs* mediocres, 2·25–2·75 mm. longi, 2–2·25 mm. lati, *subrotundo-obovati, obtusiusculi* et inferne multo angustati, in sicco apicis foveolis obscuris quam in typo minus rugosi.

Habitat in insulâ Pelagosâ grande maris Adriatici.

*F. flabellata* is recorded for Spain by Hammar on the authority of Lange, but the Spanish example so named in Lange's herbarium is *F. muralis.*

14. Fumaria purpurea Pugsley.

*Icon.* Insert "Cambridge British Flora, iii. pl. 182."

### ** Series **Macrosepalæ.**

15. Fumaria macrosepala Boissier.

This species has been lately recorded for Tlemcen, in Western Algeria. It was also found by Dr. Maire in 1923 in the interior of Morocco, on calcareous screes near Fez, and in 1925 near Taza.

*β. obscura* var. nov.

*Exsicc.* Lynes, Jebela, W. Spanish Morocco, 1923, in Hb. Mus. Brit.! Maire, Iter Maroc. nonum, in Atlantis Majoris, ditione Goundafa, 1925, in Hb. Alger.!

*Sepalis minoribus*, 4–5 mm. longis, circa 3 mm. latis, subacutis ; corollis sæpius valde rubro-tinctis ; fructibus minoribus, 2·5 mm. longis, 2 mm. latis, plane carinatis. Aliter ut in typo.

Hæc varietas per sepala minora *F. berbericam* refert, sed sepalis subintegris, petali superioris alis carinam haud æquantibus, fructibusque lævioribus distinguitur.

The plants collected by Admiral Lynes and Dr. Maire, as cited above, have sepals so much smaller than in typical *F. macrosepala* that their *facies* is very distinct and they seem worthy of varietal separation. The stations where they were obtained lie to the west and south of the range of the specific type so far as is at present known.

16. Fumaria berberica Pugsley.

This rare species was found by Dr. Maire in 1922, growing on terrace walls at Reraïa, in the Great Atlas, at an altitude of 1900 m. (probably Hooker's Revaia station) ; and in 1923, on calcareous screes above the Lac Bleu, in the Middle Atlas. The specimens from both localities, which were gathered late, are poorly grown and show no developed flowers, but their racemes, sepals, and fruits seem sufficient for identification.

### SUBSECTIO III. **MURALES.**

#### * Series **Sub-Agrariæ.**

18. FUMARIA BICOLOR Sommier. (Pl. **16**. fig. 1.)

This species is remarkable for its distribution, it being confined to the actual coasts of the Western Mediterranean, where it grows on natural ground on the cliffs. One of the pleasures of my Algerian expedition was to see it *in situ* on the sea-cliffs of Ain-Taya, east of Algiers. It occurred there on broken slopes, in soil composed mostly of loose granitic gravel, in an open association with *Asteriscus maritimus* and other maritime species. In habit it was uniformly prostrate, forming mats of various sizes, often more or less covered with the surrounding shifting gravel. It was absent from the cultivated ground near the top of the cliffs, which produced the allied *F. Bastardii* var. *Gussonei.*

In *F. bicolor* the sepals often persist on the young fruit as in *F. Bastardii.*

19. FUMARIA BASTARDII Boreau.

*Icones.* Add "Cambridge British Flora, iii. pl. 183."

A small, pale-flowered form of the type was found in garden-ground at Biskra, and var. *Gussonei* was collected in several spots near Algiers. Dr. Maire has lately sent a specimen of the type from Fez in Morocco. The variety *Gussonei* occurs also in Istria (Hb. Vindob.), and var. *patens* was collected at Mallorca by Dr. Druce in 1925.

In Hb. Haun. are two sheets, labelled in Lange's handwriting "*F. affinis* O. Hammar Monogr. Inter segetes ad Almeria, Dec. 1851," which, like that at Kew received from Lange, are typical *F. Bastardii.* Hammar's description of *F. affinis* (*F. Bastardii* var. *affinis* Pugsley) was taken from plants cultivated at Copenhagen, which were clearly not identical with these specimens but with that under the same name in Hb. Boissier.

The Hb. Mus. Brit. has recently acquired a Spanish Fumitory, sent out as a new hybrid, which seems to be a form of *F. Bastardii.* It is labelled "F. Sennen, Pl. d'Espagne, No. 3888. *F. Queri* Senn. & Pau (=*F. capreolata* × *parviflora*). Barcelone, Llobregat, 1920. Inter parentes." The specimen shows abundance of fruit, and no traces of hybridity are apparent, nor indeed anything to distinguish it from *F. Bastardii,* of which it seems a floriferous example, with long pedicels and sepals a little narrower and less toothed than usual. A further plant has subsequently been sent out by Sennen as *F. Codinæ* Sennen (=*F. flabellata* × *officinalis*)—No. 4175, Bonanova, 1921—which seems to be another form of *F. Bastardii.* This also shows an abundance of good fruit.

19*a*. FUMARIA MAURORUM Maire in Bull. Soc. Hist. Nat. Afrique du Nord, xiv. 120 (1923). (Pl. **16**. fig. 2.)

*Exsicc.* Maire, Taroudant, 1922, in Hb. Alger.!

Fumaria *habitu laxo* sæpe petiolis cirrhosis scandens. Folia irregulariter

2-3-pinnatisecta, foliolis longe petiolatis in lobos oblongos vel obovato-oblongos acutos sæpe mucronatos fissis prædita. *Racemi multiflori* (12–25-flori), tandem elongati laxiusculi, *pedunculos* mediocres *subæquantes* vel paulo longiores. *Bracteæ* lineari-lanceolatæ, acuminatæ, *pedicellis* fructiferis *suberectis*, 4–5 mm. longis, flexuosis, gracilibus, apice parum incrassatis *subduplo breviores*. *Sepala* 3–3·5 *mm. longa*, 1·5 *mm. lata*, *ovato-lanceolata*, peltata, acuminata, basin versus plus minusve *dentata*, præter nervum dorsalem latum viridem albida. *Corolla* 10–11 *mm. longa*, angusta, verisimiliter *albida*, tandem plus minusve rubescens: *petalo superiore subacuto alis roseis* vel purpureis reflexis carinam æquantibus apicemque fere attingentibus, et calcare paululum deflexo prædito; *petalo inferiore* acuto *marginibus angustis erectis vel patulis* apicem fere attingentibus; petalis interioribus apice sursum curvatis atropurpureis. *Fructûs modici*, 2–2·2 mm. longi, 2 mm. lati, *subglobosi*, parum compressi sed plane carinati, *obtusiusculi*, nonnunquam apice ipso subretusi (juniores subrostrati), inferne multo angustâti, in sicco apicis foveolis distinctis dense sed tenuiter *rugosi*.

Hæc nova species, quæ a cl. Dr. Maire ad Subsectionem *Capreolatarum* relata est, per foliorum lobos oblongos, per bracteas mediocres, per pedicellos apice parum incrassatos, et per sepala haud magna corollâ paulo angustiora ad Subsectionem *Muralium*, me judice, optime referenda est.

In hac subsectione sepala ejus relative parva, petali inferioris margines interdum patentes, et fructûs rugosi seriem *Sub-Agrariarum* præsertim referunt, sed in hac serie *F. bicolor* racemis paucifloris quam pedunculi brevioribus, bracteis parvis, sepalis minimis, corollis longius alatis, fructibusque subacutis plane differt, dum *F. Bastardii* pedunculis brevibus, bracteis latioribus cuspidatis, sepalis ovalibus serratis, corollis roseis longius alatis, fructibusque rugosioribus distinguenda est. *F. apiculata* foliorum segmentis angustioribus, pedunculis brevissimis, sepalis majoribus, fructibus ovatis apiculatis facile separari potest.

*F. rupestris* (Subsect. *Agrariæ*) propter pedicellos suberectos, cum bracteis acuminatis corollisque angustis *F. maurorum* subsimilis sed aliter omnino diversa est.

*F. maurorum* in Imperio Maroccano austro-occidentali rupes calcareas secus amnem Sous, prope urbem Taroudant, habitat.

The above description of this new Fumitory has been adopted from Dr. Maire's original careful and detailed diagnosis, collated with a specimen from Taroudant kindly supplied by him. The new plant appears, on the whole, to be most nearly allied to *F. Bastardii*, one of the most widely distributed and variable species of the genus, but it presents several essential points of distinction and cannot be held conspecific.

The addition of another species to the Section *Grandiflora* in North-west Africa is of great interest, and emphasizes the predominance of these plants in that region, where eighteen out of thirty known species have now been

recorded. It is to be hoped that Dr. Maire will also succeed in re-finding the very handsome white-flowered Fumitory of which a fragment was sent to Kew from South Morocco by Miss Bainbridge in 1907.

## ** Series **Eu-Murales.**

### 20. Fumaria Munbyi Boissier & Reuter.

In a vineyard west of Ain-Taya that appeared to have been recently weeded a single plant was seen that perhaps belongs to this rare species. Both in flower (except for less toothed sepals) and in fruit it agrees closely with the material in Hb. Boissier and with Munby's specimen at Kew, but its fruit was not regularly developed and it may possibly be a hybrid between *F. capreolata* and some other large-flowered species. The certain re-discovery of this beautiful Fumitory in Algeria is very desirable.

### 21. Fumaria Martinii Clavaud.

*Icon.* Add "Cambridge British Flora, iii. pl. 184."

The Portuguese station given in the Revision, p. 283, should be deleted, Mariz' specimen in Hb. Mus. Brit., now fragmentary, being rather a form of *F. apiculata.*

### 21*a*. Fumaria ouezzanensis sp. nov. (Pl. **16**. fig. 5.)

*Exsicc.* Maire, Iter Marocc. nonum, Ouezzan, 26 April, 1925, in Hb. Alger.!

Fumaria *satis robusta,* ramosa, nonnunquam petiolis cirrhosis scandens. *Folia* irregulariter 2-*pinnatisecta*, foliolis 3-partitis in lobos oblongos, ovatos vel late cuneatos sæpius obtusos mucronatos fissis, infimis breviuscule petiolatis, prædita. *Racemi laxiusculi*, 10–25-*flori*, *pedunculos* mediocres *subæquantes* vel paulo longiores. *Bracteæ* lanceolato-subulatæ, acuminatæ, nervo viridiusculo albidæ, *pedicellis* fructiferis 5 mm. longis tenuibus *erecto-patentibus vel apice recurvatis paulo breviores. Sepala* 3·5–5 *mm. longa,* 2–3 *mm. lata, ovato-lanceolata*, peltata, acuminata, *subintegra* vel basi parce dentata, nervo dorsali viridi albida. *Corolla magna*, 12–14 *mm. longa,* speciosa, *rosea* ; *petalo superiore obtuso*, vix dorsum compresso, *alis atropurpureis* sursum reflexis carinam excedentibus apicemque attingentibus et calcare rotundato paululum deflexo prædito; *petalo inferiore marginibus* angustis *suberectis* apicem haud attingentibus acuto ; petalis interioribus apice sursum curvatis atropurpureis. *Fructûs modici,* sine apiculo 2–2·5 mm. longi, 2–2·25 mm. lati, *subrotundo-quadrati* vel subrotundi, *obtusissimi breviter apiculati,* paulo compressi et carinati, inferne breviter contracti, siccitate apicis foveolis angustis distinctis *rugosi.*

Hæc pulchra planta *F. sepium* (præsertim var. *Gaditanæ*) verisimiliter proxima est, sed propter flores roseos petalo superiore obtuso late alato præditos et fructûs rugosos apiculatos differt.

*F. Martinii* foliorum segmentis angustioribus, pedunculis brevioribus, bracteis brevioribus cuspidatis, petalo superiore subacuto, fructibusque sublævibus facile separanda est.

*F. Munbyi* per foliorum segmenta angustiora, per sepala dentata, et per fructûs minimos sublæves cum *F. ouezzanense* confundi non potest.

*F. muralis* (sensu lato) et *F. apiculata* propter foliorum segmenta angustiora cum floribus minoribus fructibusque sublævibus longe distant.

*F. macrosepala* et *F. berberica* Subsectionis *Capreolatarum* pedicellis crassioribus, bracteis sepalisque majoribus, floribus pallidioribus, petalo superiore haud obtuso alis angustioribus prædito plane separandæ sunt.

*F. ouezzanensis* a cl. Dr. Maire in Aprili, 1925, in rupe calcareâ et in sepibus circa urbem Ouezzan in Mauritaniâ septentrionali inventa est.

This newly discovered Fumitory, when well grown, is probably one of the most beautiful in the whole genus.

22. FUMARIA SEPIUM Boissier.

This species is found to extend southwards in Morocco to the Middle Atlas. It was collected at Azrou in 1919 by Admiral Lynes (var. *gaditana*); at Boulhaut, Chaouia, in 1924, by M. Jahandiez (var. *gaditana*); and in the Zaer district to the westward in 1925 by Dr. Maire.

23. FUMARIA MURALIS Sonder.

In the Revision (p. 285) *F. capreolata β. Burchellii* DC. Syst. ii. 133 (1821) is cited among the synonyms of *F. muralis*. Burchell's South African specimen (No. 1298) at Kew, however, is not a *Fumaria*, but a fragment of *Trigonocapnos curvipes* Schlechter.

ε. *decipiens* Pugsley.

Insert "*Exsicc.* Pugsley, No. 178!"

In 1923 this variety was collected by Mr. Lacaita near Vigo, in Galicia.

γ. *cornubiensis* Pugsley in Rep. Watson Bot. Exch. Club, iii. No. 7, p. 246 (1924).

*Exsicc.* Pugsley, No. 284!

Planta habitu gracili, foliis sæpissime parvis, pedunculis pedicellisque gracilibus, et fructibus, ut in typo, minimis, subrotundis, acutiusculis, lævibus. Racemi 10–15-flori, bracteis pedicellos fructiferos fere æquantibus. Sepala 3·5–4 mm. longa, 2–2·5 mm. lata, ovata, acuta, basin versus plus minusve denticulata. *Corolla* circa 9 (raro 10) mm. longa, *pallide lilacina*; *petalo superiore lato* alis atropurpureis carinam superantibus apicemque attingentibus obtuso; calcare rotundato sepalis breviore; *petalo inferiore* angusto *marginibus patulis* sæpius apice plus minusve dilatatis *subspathulato*.

Hæc varietas in arvis prope Mevagissey in comitatu Cornubiâ Angliæ crescit.

In 1922 living material of a very distinct Fumitory allied to *F. muralis*, which had been found near Mevagissey, in West Cornwall, was received from Miss E. S. Todd, of Exeter. The following month an opportunity was taken of visiting this station, where the plant occurred abundantly over a considerable area. While the known forms of restricted *F. muralis* which diverge from the type tend to approach forms of the subspecies *Borœi*, this Mevagissey plant, owing to its uniformly small, broadly winged, and very pale-coloured flowers, in no way recalled *F. Borœi*, which grew near it, and seemed possibly a species distinct from *F. muralis*. Several of its features are exactly those of typical *F. muralis*—the essentially slender habit, small foliage, slender peduncles and pedicels with finely pointed bracts, and notably the very small, smooth, subglobose and slightly pointed fruits. Its distinctive characters lie in the corolla, which is smaller than in the known forms of *F. muralis*, being rarely more than 9 mm. long when well grown, of a very pale, lilac-pink colour, with broad, rich purple wings and a short spur to the obtuse upper petal, and spreading margins to the lower one frequently dilated towards the apex in a subspathulate outline recalling *F. officinalis*. In typical *F. muralis* the flower is full pink as in *F. Borœi*, with the wings of the apiculate upper petal not reaching the apex, and very narrow, erect margins to the lower petal with no apical dilation. The Madeiran varieties *Lowei* and *lœta* show more development of the wings of the upper petal, which often reach the apex and render it obtuse, and very occasionally the margins of the lower petal are slightly dilated about the apex. But in these varieties, although the flowers are often larger than in the type, the wings and margins are distinctly narrower than in the Mevagissey plant, and their corollas never show its unique pale colouring. The new plant is thus the most distinct from the original type of *F. muralis*. As its points of difference, however, lie almost entirely in the corolla, they seem insufficient to warrant its separation except as a variety, and it has been treated accordingly.

23*a*. FUMARIA MURALIS subsp. NEGLECTA Pugsley.

*Icon.* Insert "Cambridge British Flora, iii. pl. 185."

*Exsicc.* Pugsley, No. 285 !

After my original discovery of this plant in 1907 it was lost sight of until refound by me in September, 1922, growing with *F. Martinii* near the original station.

23*b*. FUMARIA MURALIS subsp. BORÆI Pugsley.

*Icones.* Insert "Cambridge British Flora, iii. pl. 186."

ε. *britannica* Pugsley.

Insert "*Icon.* Cambridge British Flora, iii. pl. 187—forma depauperata."

24. **Fumaria apiculata** Lange.

The herbarium at Copenhagen contains two type sheets of this plant collected by Lange at Guadarrama in 1852, and a third sheet showing a specimen cultivated at Copenhagen in 1867. Though now rather fragmentary, these exsiccata still possess both flowers and fruits. There are also several other sheets from Lange in this herbarium containing plants that seem conspecific with *F. apiculata* though differently named by Lange. Such are "*F. muralis*—Hispania," "*F. Boræi*—Ad sepes pr. Cordoba, 1852," *F. Boræi* and *F. confusa*—"Villafranca del Vierzo, 1852," and probably "*F. Thuretii*, Cadiz, 1852." A perusal of this material indicates that Lange was not familiar with the Fumitories of this group and offers some explanation of their cursory treatment in the 'Flora Hispanica.'

*F. apiculata* may be confused, not only with *F. muralis* and *F. Reuteri*, but with weak forms of *F. Martinii*, which sometimes closely resemble it. The best means of distinction are the weaker habit and narrower leaf-segments of *F. apiculata*, its more shortly peduncled racemes, suberect pedicels, smaller flowers with relatively larger and more strongly nerved sepals, and more ovate and apiculate fruits.

Another Spanish plant that recalls *F. apiculata* has lately been received in Hb. Mus. Brit. This is "Sennen, Pl. d'Espagne, No. 2217, × *F. Bonanovæ* Sen. (= *F. major* × *capreolata* ej.), Catalogne, Barcelone, près la Bonanova, talus, 3. 5. 15." Hybridity is not obvious in this specimen, which is a very large, lax plant with foliage and flowers closely resembling those of undoubted *F. apiculata*, and abundance of similar rather small and pointed fruits. It is quite unlike Verguin's × *F. Burnati* (*F. major* × *capreolata*), which has much larger flowers and is almost entirely barren, as is usual with hybrid *Fumariæ*. "Sennen, No. 2525," sent out a year later as × *F. Bonanovæ*, is a weaker form of the same plant in which no fruit was seen.

It is evident from Lange's material that *F. apiculata* is very widely distributed in Spain, ranging in the north from the province of Asturias (Cangas de Tineo) to Barcelona, and extending southward through the centre of the peninsula to the province of Andalusia. It also occurs in Portugal (Fl. Lusit. Exs. No. 594, Mariz, Pinello, 1888! and R. P. Murray, Barqueiros, 1889! in Hb. Mus. Brit.).

A fresh description of this species, which is very scarce in British herbaria, is appended:—

*F. apiculata* Lge. Ind. Sem. Haun. 23, et Ann. Sci. Nat. ser. IV. ii. 371 (1854).

Fumaria *habitu vix robusto* sæpius valde ramosa, suberecta vel diffusa, vel rarius elongata petiolis cirrhosis scandens. Folia irregulariter 2–3-pinnatisecta, foliolis in lobos sæpius parvos lanceolatos acutos vel oblongos mucronatos fissis prædita. *Racemi laxi*, 6–15- (raro 20-) *flori*, *pedunculos* sæpe brevissimos plane *superantes*. *Bracteæ* lineari-lanceolatæ, tenuiter acuminatæ, *pedicellis* fructiferis gracilibus *suberectis* (raro flexuosis vel recurvatis) paulo *breviores*. *Sepala* 3·5–4·5 *mm. longa, circa* 2 *mm. lata, ovato-lanceolata* vel ovata, basi subtruncata, vix peltata, acuta, *integriuscula* vel remote denticulata, nervo distincto viridiusculo albida, corollæ tubo latiora. *Corolla* 10–12 *mm. longa, rosea*, plus minusve angusta, parum curvata ; *petalo superiore alis atropurpureis* reflexis carinam vix æquantibus apicemque vix attingentibus *subacuto* ; calcare longiusculo deflexo ; *petalo inferiore marginibus* angustissimis *erectis vel subpatulis* acuto ; petalis interioribus apice atropurpureis sæpius fere rectis. *Fructûs modici*, circa 2·5 mm. longi, 2 mm. lati, *ovati, obtusiusculi*, per styli basin persistenter brevissime *apiculati*, paulo compressi sed obscure carinati, inferne multo angustati, siccitate apicis foveolis latiusculis paulo obscuris *sublæves*.

25. Fumaria Petteri Reichenbach.

This species is recorded for Corfu in Vierhapper's 'Flora Griechenlands,' p. 249 (1914).

### *** Series **Sub-Latisepalæ.**

26. Fumaria Thuretii Boissier.

Since the publication of the Revision additional material of this species has been seen from Istria (Vierhapper) ; of var. *deflexa* from the island Meleda, off Dalmatia (Hb. Vindob.) ; and of var. *pikermiana* from the Dalmatian Islands Lesina and Lissa (Hb. Vindob.).

27. Fumaria Reuteri Boissier.

Among the synonyms of this species shown in the Revision are *F. parviflora* var. *segetalis* Hamm. and *F. segetalis* Coutinho, the identity of the latter name with *F. Reuteri* having been confirmed by authentic material received from Prof. Coutinho. There is a sheet of good material in Hb. Haun. of the original plant on which Hammar's variety was founded, labelled by Lange, "*F. parviflora* var.? (*F. Reuteri* Boiss.) [corrected to *F. parviflora* var. *segetalis* Hamm.] Granada, inter segetes, 20. 4. 52." This material is not identical with Coutinho's species or with *F. Reuteri*, but is clearly near *F. parviflora*, with pink flowers about 6 mm. long. Its outer petals are less broadly winged than in ordinary *F. parviflora*, and the sepals are much larger, about 1·5 mm. long, and nearly orbicular. The fruit is entirely abortive, undeveloped ovaries still remaining on most of the pedicels. The plant is evidently a barren hybrid between *F. parviflora* and another small-flowered species, which, judging from the relatively large and broad sepals, is *F. micrantha*. A second sheet in Hb. Haun. showing a cultivated example similarly named, said to have been raised from seed of the Granada plant, appears to be a form of true *F. parviflora*, and obviously was not obtained from the hybrid. *F. parviflora β. segetalis* Hamm. Mon. 17, and Willkomm & Lange, Fl. Hisp. iii. 885, should therefore be deleted from the synonymy of *F. Reuteri*.

*F. Reuteri* was collected by Mr. Lacaita in 1923 in the Sierra Morena, to the north of Andalusia.

### SECTIO II. PARVIFLORA.

### SUBSECTIO IV. **LATISEPALÆ.**

30. FUMARIA MICRANTHA Lagasca.

*Icones.* Insert "Cambridge British Flora, iii. pl. 188."

31. FUMARIA BRACTEOSA Pomel.

β. *emarginata* var. nov.

*F. emarginata* Braun-Blanquet in Bull. Soc. Hist. Nat. Afrique du Nord, xiii. 13 (1922).

*Exsicc.* Braun-Blanquet, Sidi Bou Othmane, in Hb. Zurich.

*Fructibus* apice rotundatis breviter *emarginatis* sinu acuto triangulari subcompressis a typo differt.

Inter segetes prope Sidi Bou Othmane (Djebilet) in Mauritaniâ habitat.

This plant, described as a new species by Dr. J. Braun-Blanquet, seems to differ from *F. bracteosa* only in the form of its fruit, and has accordingly been reduced to varietal status. Dr. Maire concurs in this view.

### SUBSECTIO V. **OFFICINALES.**

33. FUMARIA OFFICINALIS Linn.

*Icones.* Insert "Cambridge British Flora, iii. pl. 189."

### SUBSECTIO VI. **MICROSEPALÆ.**

#### * Series **Ambiguæ.**

38. FUMARIA AUSTRALIS Pugsley.

This species has been collected in a fresh station in the Kyimbila district, north of Lake Nyasa (Stoltz, 1914, No. 2503 !).

38 *a.* FUMARIA ALGERIENSIS sp. nov. (Pl. **16**. fig. 3.)

*Exsicc.* Pugsley, Nos. 286 ! and 292 ! Jahandiez, Pl. Marocc. 1924, No. 962 *b*, Moyen Atlas, Col du Taghzeft, in Hb. Mus. Brit., ut *F. Pugsleyana* (partim) !

Fumaria *habitu nano robusto*, sæpius e basi ramosa, suberecta vel adscendens, verisimiliter haud scandens. *Folia* glauca, *multa subradicalia* longe petiolata ut in genere *Rupicapnos*, caulina inferiora longe petiolata, superiora brevius petiolata ad subsessilia, omnia 2–3-pinnatisecta, foliolis nunc breviuscule petiolatis confertis nunc laxioribus, in *lacinias* planas *lanceolatas* acutas vel oblongas mucronatas fissis, prædita. *Racemi* 12–25-flori, *densissimi*, *pedunculos brevissimos* crassos *multo superantes*. *Bracteæ latæ*, oblongæ, cuspidatæ, nervo viridiusculo albidæ, *pedicellis* fructiferis *brevissimis* (1·5–2 mm. longis) crassiusculis *erecto-patentibus paulo longiores*. *Sepala* 1·5–2 *mm.*

*longa*, 1 *mm. lata, oblongo-ovata*, peltata, breviter acuminata, plus minusve *irregulariter dentata*, præter nervum angustum viridiusculum albida. *Corolla circa* 5 *mm. longa, albida,* plus minusve roseo-tincta ; *petalo superiore alis roseis* vel purpureis crenatis sursum reflexis carinam viridem crassam subtruncatam subæquantibus et apicem attingentibus *obtuso* vel rarius retuso, calcare breviusculo adscendente ; *petalo inferiore* marginibus roseis vel purpureis patentibus apicem attingentibus obtusiusculo *spathulato* ; petalis interioribus latiuscule alatis apice purpureis *Fructûs modici*, 2–2·25 mm. longi ac lati, *subrotundo-ovati*, *obtusi*, inferne in stipitem latum parum angustati, paululum compressi et satis carinati, siccitate apicis foveolis paulo obscuris *dense rugosi*.

Hæc *Fumaria* per habitum ramis curtis nanum robustum et per folia inferiora longe petiolata laciniis confertis prædita notabilis est. Inter generis alias species *F. abyssinicam* et *F. parvifloram* maxime refert, sed ab illâ habitu multo robustiore, foliorum segmentis crassioribus haud aristatis, racemis densioribus, bracteis latioribus, sepalis relative majoribus magis peltatis, corollis pallidioribus, fructibus haud apiculatis distinguitur, ab hac foliorum segmentis latioribus, racemis densioribus, sepalis multo majoribus, petali superioris alis roseis vel purpureis sursum reflexis, fructibusque minus carinatis plane differt.

*F. algeriensis* apud ruinas oppidi Romani Timagudi, et in rupibus montis Djebel Tougour provinciæ Constantinæ, prope Bedeau provinciæ Oranensis, atque probabiliter in aliis locis regionis " Hauts Plateaux " in Algeriâ crescit ; etiam ad Col du Taghzeft in regione Maroccanâ Moyen Atlas.

This inconspicuous species was found in 1922 in small quantity among the ruins of Timgad, where it was growing in company with *F. officinalis.* Afterwards it was seen very sparingly on the lower rocks of Djebel Tougour, close to a station for *Rupicapnos Cossonii*, and since my return from Algeria it has been sent by M. d'Alleizette from the Hauts Plateaux region in the province of Oran. Still later, M. Jahandiez has found it in the Moyen Atlas of Morocco. It is not unlikely that it will prove to be widely distributed in the high central region of Algeria and of Morocco.

*F. algeriensis* is perhaps most closely allied to *F. parviflora*, but its much larger sepals and the form of its corolla preclude its inclusion among the *Eu-Microsepalæ*, and it therefore seems best placed among the *Ambiguæ* after *F. australis.*

### 39 *a.* FUMARIA CAROLIANA sp. nov. (Pl. **16**. fig. 4.)

*Exsicc.* Pugsley, No. 288 !

Fumaria *gracilescens*, satis ramosa, suberecta vel diffusa. *Folia* viridia, foliolis in *lacinias* planas *lanceolatas* vel lineari-oblongas, acutas vel mucronatas fissis 2–3-pinnatisecta, eis *F. officinalis* var. *Wirtgenii* subsimilia. *Racemi laxiusculi*, 10–15- (rarius 20-) flori, *pedunculos* breves graciles *multo* *superantes. Bracteæ* lineari-lanceolatæ, tenuiter acuminatæ, *pedicellis* fructiferis *suberectis* gracilibus flexuosis 4–5 *mm. longis* apice paulo incrassatis fere *dimidio breviores. Sepala* 1·5–2 *mm. longa,* ·75–1 *mm. lata, ovato-lanceolata* vel oblonga, longe acuminata, plus minusve *irregulariter inciso-dentata,* nervo viridiusculo rosea, diu persistentia. *Corolla* 6–7 *mm. longa* (in racemis primariis forsitan longior), *rosea* ; *petalo superiore* vix lato *alis* subserratis *roseis* sursum reflexis carinam excedentibus apicemque attingentibus *obtuso* haud spathulato, calcare mediocri curvato ; *petalo inferiore* marginibus subserratis patulis roseis apicem vix attingentibus *obtusiusculo ovato-spathulato* ; petalis interioribus apice atropurpureis. *Fructûs mediocres,* circa 2 mm. longi, 2·25 mm. lati, *subrotundi,* circa medium latissimi, superne cum apiculo brevissimo obsoletove *rotundato-obtusi* sed haud truncati (juniores plane apiculati), inferne in stipitem angustissimum valde contracti, paulo compressi et obscure carinati, siccitate apice foveolis latiusculis *dense rugosi.*

Habitat in arvis inter Arras et Marœuil Galliæ borealis.

Hæc *Fumaria* quam ut speciem novam dubitanter secundum exemplaria imperfecta descripsi, verisimiliter inter *F. Schleicheri* et *F. Vaillantii* (præsertim var. *Chavinii*) fere medium tenet, sed sepala ejus majora fructûsque latiores *F. officinalem* var. *Wirtgenii* etiam referunt. Propter fructûs formam rotundatam in Subsectione *Microsepalarum* collocata est.

Per bracteas longiores, per sepala majora diu persistentia, per corollas majores petali superioris alis roseis subserratis præditas, et per fructûs latiores inferne multo angustatos a *F. Schleicheri* differt.

*F. Vaillantii* et *F. Schrammii* pedicellis brevioribus, sepalis minimis, corollis brevioribus, petali superioris emarginati alis subpatentibus plane separandæ sunt.

*F. officinalis* var. *Wirtgenii* habitu robustiore, pedicellis brevioribus, sepalis caducis, corollis latioribus, petali superioris alis purpureis subpatentibus potiusquam roseis sursum reflexis, fructibus apice truncatis distinguitur.

This Fumitory was noticed in June 1921, between Arras and Marœuil, on a visit to the grave of my eldest son, Charles Clifford, who was killed in 1916 in the Great War ; and I venture to commemorate him in naming it, for he was a keen and promising naturalist, who contrived to send me specimens of *Fumariæ* (*F. officinalis* and *F. micrantha*) from the trenches of the battle-line in this neighbourhood shortly before his death.

When first observed, *F. Caroliana* was thought, from the colour of its flowers, to be a very small-flowered form of *F. Bastardii*, but a cursory examination sufficed to show that it was a member of the Section *Parviflora.* The plants seen had already been in flower for some time, and on some of the racemes a few fruits remained undeveloped, suggesting a hybrid parentage. If this is the origin of *F. Caroliana*, one of the parents should

be *F. Schleicheri*, which has similar racemes of very long-pedicelled flowers. But the new plant had developed plenty of good fruit, and there seem no certain indications of hybridity.

In its combination of flowers nearly as large as those of *F. officinalis* with *Vaillantii*-like fruits, *F. Caroliana* recalls Koch's description of his *F. Wirtgenii* (Syn. Fl. Germ. ed. 2, App. p. 1018), but the specimens in herbaria under this name, including the material sent out by Wirtgen himself (No. 158, Coblentz, etc.), possess corollas and fruits which clearly resemble those of *F. officinalis*, to a variety of which Haussknecht, with apparent reason, reduced Koch's species.

In the summer of 1923, on a second visit to Arras, this rare plant was sought on the same spot, but the only form found was a curious, slender plant with similar rounded, apiculate fruits only partially developed and the flowers of *F. officinalis*. This has the aspect of a hybrid *F. Caroliana* × *officinalis*, and in some respects resembles the variety *Wirtgenii* of the latter.

### ** Series **Eu-Microsepalæ**.

43. FUMARIA VAILLANTII Loiseleur.

*Icones.* Insert "Cambridge British Flora, iii. pl. 190."

In Hb. Haun. there is a specimen of this plant from Lapland.

γ. *Chavinii* Rouy & Foucaud.

The exsiccata "Bourgeau, Pl. d'Espagne, No. 2108," cited under this variety, is a difficult plant which may indicate a transition to *F. Schrammii* by its relatively straight corolla-spur and very small rotundate fruits.

ε. *maroccana* var. nov.

*Exsicc.* Jahandiez, Pl. Marocc. 1924, No. 551. Bekrit, Moyen Atlas, in Hb. Mus. Brit.!

Planta varietatis *Chavinii* habitu foliisque. *Racemi multi-* (ad 20-) *flori*, densiusculi, brevissime pedunculati. Bracteæ angustæ, pedicellis brevibus (2 mm. longis) gracilibus tertiâ parte breviores. Sepala facile caduca. *Corolla parva*, circa 5 mm. longa, *purpureo-rosea*, *petalo superiore alis roseis* angustis calcareque longo adscendente. *Fructûs parvi*, vix 2 mm. longi ac lati, *subrotundi*, obtusissimi, haud apiculati, apicis foveolis distinctis rugosi.

Hæc planta varietati *confertæ* proxima videtur, sed racemis pedicellisque longioribus, corollis purpurascentibus magis diffusa est. *Fumariæ Schrammii* etiam faciem habet, sed habitu robustiore, corollæ calcare curvato adscendente, fructibus sine apiculo obtusis differt.

The occurrence of this plant in Morocco is of special interest as a confirmation of the old record by John Ball.

44. FUMARIA SCHRAMMII Velenovsky.

This plant was treated as of specific rank in the Revision but was erroneously shown as sp. nov. It had already appeared as a distinct species in Velenovsky's 'Flora Bulgarica,' and should have been cited as "*F. Schrammii* Velen. Fl. Bulg. p. 22 (1891)."

*β. Pugsleyana* Maire MS.

*Exsicc.* Maire, Timhadit, Moyen Atlas, Morocco, 1923, in Hb. Alger.! Jahandiez. Pl. Marocc. 1924, No. 962 *b*, Col du Taghzeft, in Hb. Mus. Brit., ut *F. Pugsleyana*, partim!

Planta habitu humili ramosissimo. *Bracteæ* lineari-lanceolatæ, acuminatæ, plus minusve denticulatæ, *pedicellos crassos brevissimos* (circa 1 mm. longos) *æquantes*. Sepala minutissima, ad ·4 mm. longa, laciniata, sæpe trifida. *Corolla albida*, petalorum exteriorum *alis* marginibusque subpatentibus quam in typo *latioribus*. *Fructûs* circa 2·25 mm. longi, 2 mm. lati, *subrotundo-ovati*, plane apiculati, parum compressi et vix carinati, *rugosi*. Aliter ut in typo.

Hæc varietas propter corollam albidam late alatam speciem orientalem *F. asepalam* referentem notabilis est.

This new plant, which Dr. Maire was at first disposed to regard as a distinct species, has been inserted here as a variety under his name. It is included in his next list of Moroccan plants, which is likely to be published before this paper. The material seen is not entirely satisfactory owing to being gathered late, but the plant seems too near to typical *F. Schrammii*, especially in the form of its corolla, to be treated as a separate species.

The discovery of a form of *F. Schrammii* in a natural habitat (basaltic rocks) in the interior of Morocco is of considerable interest, for although known in Spain, this species has not previously been recorded for North Africa.

46. FUMARIA PARVIFLORA Lamarck.

The sheet of Fl. Exsicc. Austro-Hungarica, No. 87, in Hb. Haun. shows apiculate fruits and belongs to the specific type rather than to forma *Vivianii*.

*β. Symei* Pugsley.

*Icon.* Insert "Cambridge British Flora, iii. pl 191."

A plant collected in garden ground at Biskra, S. Algeria, tends towards this variety in its subemarginate fruits, but otherwise resembles the type.

*ε. glauca* Clavaud.

This variety, of which examples were obtained at Maison Carrée, near Algiers, has the wings of the upper petal not only broader but more reflexed upwards than in other forms of the species.

Hammar's variety *segetalis* (a hybrid) is dealt with above under *F. Reuteri*.

Dr. Maire has been good enough to send a portion of the type of *F. Trabutii* Battandier, which shows it to be a form of *F. parviflora* with large fruits and relatively broad leaf-segments. This was the subsequent view of the late Dr. Battandier.

## RUPICAPNOS.

*Rupicapnos* Pomel (p. 328 of Revision).

l. 15. After "gibbum" insert "viridem."

l. 18. After "gibbum" insert "viridem."

The species of *Rupicapnos* seen in their native habitats in good quantity and condition were:—*R. longipes* (*Muricaria*) at Elkantara, *R. numidica* (*Tripteryx*) at Constantine, and *R. cerefolia* (*Callianthos*) at Milianah. *R. sarcocapnoides* (*Sarcocapnoides*) was unfortunately missed on Djebel Tougour.

The flowers of the three first-named species, when fresh, are so absolutely dissimilar that the creation of their generic Sections is abundantly justified on this ground without reference to other organs. The open corolla of *R. longipes*, like that of *R. sarcocapnoides*, recalls certain species of *Sarcocapnos*; the tiny flattened flower of *R. numidica* has the aspect of a miniature unopened *Sarcocapnos*, with three pairs of wings instead of two; and *R. cerefolia* resembles a large-flowered *Fumaria* such as *F. agraria*. It was noticed at Milianah that in the finest flowers of *R. cerefolia* the winged dorsal nerve of the purple-tipped inner petals tended to produce a narrow white margin, which appears to be further developed in *R. ochracea*; and this seems to indicate a transition towards the three-winged corolla characteristic of the Section *Tripteryx*.

In the Revision the annual species are grouped together in one Section, following Pomel's arrangement, but it is clear from a subsequent examination of the type of *R. delicatula* that, both in corolla and in fruit, it resembles the species of the Section *Tripteryx*, as was suggested, and its stations fall within the range of that Section. Other more recently discovered North African annual forms which possess the corolla and fruit of the Section *Callianthos* and inhabit the same geographical area have been received through the kindness of Drs. Battandier and Maire.

It thus seems that all the annual species do not naturally fall into one separate group, and therefore, with the concurrence of Dr. Maire, the definitions of the two Sections *Tripteryx* and *Callianthos* have been extended to include annual species, leaving *Muricaria* to represent the Saharan forms. Of these plants, *R. longipes*, especially its variety *eikantarica*, produces a corolla of distinct *Sarcocapnoides* form, and hence might be transferred to that Section. It is probable too that in *R. muricaria* and the two remaining annual species included in its Section, the corolla is also really of the same form though with less dilation of the outer petals, and if so, the whole Section *Muricaria* could perhaps be reduced to a subdivision of *Sarcocapnoides*, to which it is evidently most closely related. But the fruits of the species of *Muricaria* seem very distinct, and their geographical range lies outside that of *Sarcocapnoides*, so far as is at present known, these delicate annuals inhabiting the hot regions of no great altitude bordering on the Sahara. It therefore appears best on the whole to retain *Muricaria* as a separate Section. It has been found necessary to re-arrange the perennial species of *Callianthos*.

The difference of duration of life-cycle in the species of *Rupicapnos* is of less taxonomic importance than might appear at first sight, for none of them are true perennials, capable of producing fresh shoots from the rootstock for an indefinite period. The so-called perennial species sometimes flower in their first year, as was observed with *R. cerefolia* at Milianah. They usually survive the winter, and continue their growth during the second and succeeding years by a prolongation and branching of the main axis, until they reach a stage of exhaustion or, owing to some unfavourable conditions die. In the great majority of cases the plant's life is probably limited to a very few years. The uniformly annual character of the species of *Muricaria* may be attributed to the hotter and drier climate of their habitats, which prevents their survival through the summer months.

As more material of this genus is collected, it becomes increasingly evident, as has been pointed out by Dr. Maire, that a very large number of differing but closely allied forms exist, whose status it is not easy to fix, and that while the generic sections are sufficiently well marked, the limitation of the species is often not readily determined. From the nature of the fruits and the plants' curious method of sowing their own seeds by deflexion of the fruiting pedicels, it would appear that their means of dispersal are very limited ; and the nature of the habitats—vertical rocks fissured with deep clefts—is such that they generally grow isolated in small and widely separated stations. In these stations they have probably existed for very long periods, during which, owing to environment and continued isolation, they have developed special individual features, with the result that a form discovered in any fresh locality is generally found to present points of difference from its nearest allies, and the determination of its taxonomic position is sometimes difficult. It is thus possible that, as more new forms are discovered, further re-arrangement of the generic groups may become necessary.

### Sectio I. MURICARIA.

2. **Rupicapnos delicatula** Pomel.

This species is transferred to the Section *Tripteryx* (No. 12 *a*), q. v.

3. **Rupicapnos longipes** Pomel.

The Copenhagen Museum possesses two sheets of Balansa's original gathering of this plant at Mnechounès, and although the specimens now show but few fruits and only one flower, it is possible to determine all of them as true *R. longipes*, there being no mixture like that on the Paris sheet.

A special journey to Mnechounès was undertaken in the hope of finding the three species which appear together in the Paris collection, but without success. Balansa's plants are stated to have been collected on the rocks of the great canyon of Mnechounès, into which I penetrated till continuous wading was necessary. But only a solitary specimen of *R. longipes* was found, with imperfect flowers but unmistakeable by its fruit. It is no doubt very easy to extirpate any *Rupicapnos* when it is within reach, and earlier botanists may have taken all they could find in this locality. The unusually dry season of 1922 in Algeria, however, may have affected the growth of these plants, and it is likely that they may still exist in the less accessible parts of the canyon, which is of considerable length with walls of great height.

At Elkantara, fortunately, a fair quantity of *R. longipes* was found in good flower. It is a delicately beautiful little plant, with finely coloured corollas approaching in form those of the Section *Sarcocapnoides*. In the developed flower the corolla is widely expanded by the whole upper petal being strongly reflexed upwards and the large lower petal deflexed—an outline not visible in the exsiccata previously examined owing to pressure and the disappearance of the maturer flowers, as so commonly happens in dried material of this family. The younger flowers of the Elkantara plant, however, very fairly match those in the figure of *R. longipes* from Mnechounès in the Revision, so that the same development may be assumed to take place in both. In its flowers, *R. longipes*, as a whole, clearly differs from *R. muricaria* and *R. prætermissa* by the greater apical dilation of the outer petals, and especially of the lower one, and in this respect it approaches the Section *Sarcocapnoides*.

There is a marked difference between the fruit of the Elkantara plant and that of the type of *R. longipes* from Mnechounès, the former being smaller and obovate rather than subrhomboid, with its beak reduced to a short mucro. On this ground it may be distinguished as a variety, thus:—

β. *elkantarica* var. nov. (Pl. **16**. fig. 6 A.)

*Exsicc.* Pugsley, No. 287!

Habitu foliisque læte viridibus ut in typo, sed pedunculis brevioribus (ad 20 mm. longis), bracteis apice tridentatis, pedicellis fructiferis ad 30 mm. longis. Sepala nonnunquam paulo dentata. Corolla 8–9 mm. longa, alba; *petalo superiore* marginibus latis patentibus prædito, retuso, *apicem versus læte purpureo*, externe sensim albescente, tandem *valde sursum reflexo*, calcare rotundato vix deflexo; *petalo inferiore quam superius plane longiore*, apice *in limbum* magnum *suborbicularem* emarginatum planum roseo-tinctum *abrupte dilatato* tandem deflexo, basi gibboso; petalis interioribus fere rectis apice atropurpureis quam exteriora multo brevioribus. Stylus malleiformis lobis divaricatis. *Fructûs* verisimiliter circa 2·5 mm. longi, 2·25 mm. lati; *sub-*

*rotundo-obovati, cum mucrone brevi obtusissimi,* conspicue compressi, quam in typo minor et tenuius tuberculato-rugosi.

Descriptio Elkantaræ ex exemplariis vivis facta est.

The trivial epithet for this species—*longipes*—has reference not so much to the length of the fruiting pedicels as to that of the root, which may be several times as long as the remainder of the plant. Specimens with the root (which is branched only towards its apex) intact can be readily drawn from the light soil of the deep rock-clefts wherein these plants grow.

### SECTIO II. SARCOCAPNOIDES.

7. RUPICAPNOS REBOUDIANA Pomel.

In the spring of 1925 a beautiful *Rupicapnos* was collected by Dr. Maire on the calcareous rocks of Djebel-Bou-Hellal (alt. 1550 m.) in the district of Bou-Taleb, in South Algeria. It is a form of *R. Reboudiana*, the type of which was originally found in the same district.

While generally agreeing with Pomel's original description of *R. Reboudiana*, Dr. Maire's plant can hardly be described as "fragile," and its sepals are not strongly toothed.

It is therefore treated as a variety, thus:—

*β. pulchella* var. nov.

*Exsicc.* Maire, Djebel-Bou-Hellal, May 1925, in Hb. Alger.!

Planta satis robusta, caudice brevi ramoso caulibusque brevissimis prædita. *Folia* 3–8 cm. longa (petiolo incluso), *subdeltoidea* foliolorum *segmentis* nonnunquam *acutis vel mucronatis. Racemi* densi, *multi-* (10–25-) *flori*, breviusculi, *folia subæquantes* vel breviores. *Bracteæ* circa 1·5 mm. longæ, sæpius *apice dentatæ* ; *pedicelli fructiferi filiformes*, apice paulo incrassati, flexuosi, *infimi ad* 25 *mm. longi. Sepala circa* 2 *mm. longa*, 1·5 *mm. lata, late ovata*, peltata, subacuta, *subintegra* vel leviter dentata, alba. *Corolla* 9–10 *mm. longa*, carinis latis viridiusculis *roseo-albida* ; *petalo superiore* apice *in limbum* lilacinum *suborbicularem* retusum ultra carinæ apicem productum *tandem sursum reflexum dilatato, calcare magno* adscendente rotundato ; *petalo inferiore* apice *in limbum* magnum dilute lilacinum *suborbicularem* emarginatum *dilatato, basi saccato* ; *petalis interioribus* fere rectis *apice* modice alatis *atropurpureis. Fructûs parvi, angusti*, sine mucrone 2·5 mm. longi, 1·5 mm. lati, *oblongo-obovati, obtusiusculi* et *valde mucronati*, inferne attenuati, satis compressi et carinati, in sicco omnino *dense tuberculato-rugosi.*

Hæc varietas in rupibus calcareis Djebel-Bou-Hellal in montibus Bou-Taleb Algeriæ australis crescit.

### SECTIO III. TRIPTERYX.

To include the annual species *R. delicatula*, transferred from the Section *Muricaria*, the sectional diagnosis should stand as "Plantæ perennes decumbentes *vel raro annuæ suberectæ.* Racemi multiflori, *raro pauciflori* . . . ."

In this, as in the other Sections, the tip of the inner petals is more or less purple, but this colouring is obscured or rendered obsolete through the remarkable development of the winged median nerve, which is always whitish in colour.

### SUBSECTIO **PERENNES**.

Plantæ decumbentes. Racemi multiflori.

8. RUPICAPNOS NUMIDICA Pomel.

This species, which still grows in fair quantity on the shady rocks of the Rummel gorge at Constantine, was just come into flower on 1st April, 1922. When fresh, the flat, compressed corolla is white with green keels to the two outer petals, and a purplish tip to the connate inner ones which is quite obscured by their very large white dorsal wings. These wings of the inner petals in the living state are regularly transversely fluted or undulate—a peculiarity not noticeable in dried specimens. The very short spur of the upper petal is more rounded and ascending than appears in the figure in the Revision (Pl. 9. fig. 6). The style is clearly furcæform, *i. e.* with ascending lobes. In large plants more than usually shaded the segments of the long and lax leaves become more or less acute.

12. RUPICAPNOS EROSA Pomel.

In this species, especially the variety *major*, the style is less furcæform than malleiform with more or less spreading lobes. Its characters appear to be in some degree transitional towards the Section *Callianthos*.

### SUBSECTIO **ANNUÆ**.

Plantæ suberectæ. Racemi pauciflori.

12 *a*. RUPICAPNOS DELICATULA Pomel.

At page 332 of the Revision this species was provisionally adopted in the Section *Muricaria*, but attention was drawn to its resemblance in some features to *R. tenuifolia*. Recently, through the kindness of Dr. Maire, Pomel's type has been examined, and from this it is evident that the corolla of *R. delicatula*, although an annual plant, is of *Tripteryx* form, and its fruit less compressed, with thicker and more uniformly tuberculate pericarp, than in the species of *Muricaria*.

*R. delicatula* is therefore transferred to the Section *Tripteryx*, as a solitary member of a Subsection *Annuæ*, and a revised diagnosis, taken from Pomel's material, is substituted, thus:—

*R. delicatula* Pomel, Nouv. Mat. Fl. Atlant. i. 246 (1871).

*Exsicc.* Pomel, Ksar-el-Maia, 1862, in Hb. Alger.!

Rupicapnos *annua*, radice longâ et caule gracillimo suberecto ad 5 cm. alto vix ramoso prædita. *Folia* omnia caulina, longissime petiolata, cum

petiolo ad 6 cm. longa, *subdeltoidea, foliolis* sæpius 2-paribus infimis longiuscule petiolatis et segmentis secundariis *in lacinias parvas lineari-oblongas* (oblongas in foliis primariis) *subacutas* plus minusve divaricatas irregulariter *fissis 2–3-pinnatisecta. Racemi pauci-* (2–10-) *flori*, breviter pedunculati, *foliis plus duplo breviores. Bracteæ* circa 1 mm. longæ, *lanceolatæ*, acutæ, subintegræ ; *pedicelli fructiferi filiformes* apice incrassati, *sub-* 10 *mm. longi. Sepala* 1 *mm. longa,* ·5 *mm. lata, lanceolata*, vix peltata, acuminata, *denticulata*, albida. *Corolla minima, circa* 4 *mm. longa*, relative gracilis, præter carinas virides *albida* ; *petalo superiore* apice marginibus latiusculis patentibus *anguste obovato obtusissimo, calcare brevi* (1 mm. longo) angusto fere recto ; *petalo inferiore* marginibus latiusculis patentibus *subspathulato subtruncato*, basi haud saccato ; *petalis interioribus* fere rectis apice verisimiliter obscure purpureis *alâ latâ* albidâ inter petalorum exteriorum margines quos fere æquat subpatulâ præditis. Stylus verisimiliter furcæformis. *Fructûs modici,* circa 2 mm. longi ac lati, *subrotundi, cum mucrone brevi* quadrato *obtusiusculi*, inferne multo angustati, parum compressi sed plane carinati, in sicco omnino *dense tuberculato-rugosi* muricati.

This plant is still known only from the original station at Ksar-el-Maia.

## Sectio IV. CALLIANTHOS.

Since the Revision was written several fresh forms belonging to this Section have been brought to notice, and Pomel's types not previously seen have been examined. Two annual plants are now known whose flowering and fruiting characters are those of *Callianthos*, and not of *Muricaria*, and whose habitats fall within the geographical range of the first-named group. The addition of these plants necessitates the division of the Section into two Subsections, *Perennes* and *Annuæ*, as in the *Tripteryx* group; and the Sectional diagnosis will accordingly need the following emendation :—
" Plantæ perennes decumbentes *plus minusve carnosæ* eis sectionum aliarum *sæpius* majores, *aut annuæ parvæ suberectæ parum ramosæ.* Racemi multiflori *vel rarius pauciflori.* Flores *parvuli ad maximi*, 9–16·5 mm. longi, . . . . Fructûs *parvi* ad maximi."

The diversity of form obtaining among the perennial species now known makes it also desirable to re-arrange this subgroup, and a fresh clavis is therefore inserted to supersede that at page 330 of the Revision.

## Section IV. CALLIANTHOS.

Decumbent perennial plants, ± fleshy and often larger than those of the other Sections, with 2-3-pinnatisect and mostly subradical leaves and many-flowered racemes, or dwarf, slender, suberect, slightly branched annuals with few-flowered racemes. Flowers rather small to very large, 9–16·5 mm. long, white or pale purple; outer petals never apically

dilated into a spreading suborbicular limb, little exceeding the inner petals, which are tipped with dark purple and not broadly winged; lower petal + saccate. Fruit small to very large.

### Subsection PERENNES.

Perennial, ± fleshy plants. Racemes many-flowered.

#### Series CEREFOLIÆ.

Leaves deeply divided into numerous small or narrow ultimate segments, with ± slender petioles. Flowers whitish except in typical *R. ochracea.*

13. *R. ochracea.* Plant dwarf; leaves oblong-deltoid, with small segments. Flowers smaller than in succeeding species of Subsection. Sepals small, ovate or lanceolate, dentate. Corolla with long, slender spur. Fruit small, oblong-elliptic, long-mucronate.

14. *R. graciliflora.* Leaves oblong or oblong-deltoid, with narrow segments. Sepals ovate-lanceolate, subentire. Corolla slender, with long, narrow spur. Fruit of moderate size, oblong-elliptic, submucronate.

15. *R. platycentra.* Plant dwarf; leaves oblong-deltoid, with small segments. Sepals suborbicular, dentate. Corolla with large, broad spur. Fruit large, ovate-elliptic, short-mucronate.

16. *R. cerefolia.* Leaves oblong, with narrow segments. Sepals ovate, dentate. Corolla very large, with long spur. Fruit very large, obovate-elliptic, strongly keeled and mucronate.

#### Series AFRICANÆ.

Leaves less deeply divided into fewer larger or fairly broad ultimate segments, usually with stout petioles. Flowers whitish.

17. *R. speciosa.* Leaves oblong, with oblong segments. Sepals subrotund-ovate, dentate. Corolla large, with rather short spur. Fruit rather large, oblong-elliptic, long-mucronate.

18. *R. Mairei.* Leaves thick, narrowly oblong, with short segments. Sepals orbicular, dentate. Corolla rather slender, with large spur. Fruit large, subrotund-obovate, submucronate.

19. *R. africana.* Leaves thick, oblong-deltoid, with oblong segments. Sepals ovate, dentate. Corolla large, with moderate spur. Fruit large, subrotund-ovate, long-mucronate.

20. *R. decipiens.* Leaves thick, deltoid, with short segments. Sepals ovate, dentate. Corolla large, with moderate spur. Fruit typically very large, subrotund or obovate, strongly mucronate.

#### Series POMELIANÆ.

Leaves still less deeply divided into fewer, large and broad ultimate segments, with stout petioles. Flowers pale purple.

21. *R. Pomeliana.* Leaves thick, oblong, with very broad segments. Sepals suborbicular, dentate. Corolla large, with very short spur. Fruit rather large, subrotund-obovate, short-mucronate.

22. *R. oranensis.* Leaves thick, oblong, with less broad segments. Sepals ovate, subdentate. Corolla very large, with rather large spur. Fruit large, oval-obovate, strongly mucronate.

### Subsection ANNUÆ.

Annual, not fleshy plants. Racemes few-flowered.

| | |
|---|---|
| 23. *R. gaetula.* | Leaves oblong-deltoid, 2-pinnatisect, with oblong segments. Corolla large, very slender, with very long, curved spur. |
| 24. *R. fraterna.* | Leaves deltoid, 2-trisect, with lanceolate segments. Corolla rather small, with short, straight spur. |

### SUBSECTIO **PERENNES.**

Plantæ perennes, ± carnosæ. Racemi multiflori.

#### * Series **Cerefoliæ.**

Folia in segmenta numerosa parva vel angusta alte fissa, petiolis plus minusve gracilibus prædita. Flores albidi nisi in *R. ochraceâ.*

13. RUPICAPNOS OCHRACEA Pomel.
*Vide* p. 351 of Revision.

*β. Battandieri* var. nov.

*Exsicc.* Battandier, Djebel Antar, 1888, in Hb. Alger.! Pugsley, No. 289!

Rupicapnos perennis caudice crassiusculo decumbente brevissime ramoso vestigiis petiolorum emarcidorum donato, caulibus verisimiliter brevissimis. *Folia* subradicalia, plus minusve glaucescentia, relative *nana*, 4–6 cm. longa (petiolo 3–4·5 cm. incluso), *oblongo-deltoidea*, foliolis sæpius 3-paribus subdeltoideis brevissime petiolatis et segmentis secundariis subflabellatis in *lacinias* confertas *parvas oblongas subacutas* irregulariter fissis 2-*pinnatisecta*. *Racemi* corymbiformes, *multi-* (10–20-) *flori*, cum pedunculo (ad 3 cm. longo) *folia* sæpius *subæquantes*. *Bracteæ* 1–2 mm. longæ, *lineari-oblongæ*, cuspidatæ, subdentatæ ; *pedicelli fructiferi filiformes*, apice paulo incrassati, flexuosi, *infimi ad 35 mm. longi*. *Sepala circa* 1·5 *mm. longa*, 1 *mm. lata*, *subrotundo-ovata*, peltata, acuta, irregulariter *valde dentata*, albida, corollæ tubum latitudine æquantia. *Corolla* 9–12 *mm. longa*, gracilis, verisimiliter *albida* ; *petalo superiore* marginibus apicem versus paulo dilatatis subpatentibus *angusto oblongo obtuso*, *calcare longo* (ad 4 mm.) curvato paulo deflexo ; *petalo inferiore* marginibus latiusculis patentibus apice sensim dilatatis *lineari-spathulato obtusiusculo*, *basi obscure saccato* ; *petalis interioribus* sursum curvatis *apice alâ* dorsali conspicuâ *albidâ purpureis*. *Fructûs parvi*, 2–2·25 mm. longi (sine mucrone) et 1·5–1·75 mm. lati, *oblongo-elliptici*, *cum mucrone magno acutiusculi*, inferne in stipitem distinctum angustati, multo compressi sed obscure carinati, siccitate omnino *dense tuberculato-rugosi*.

Hæc planta, cl. Dr. Battandier monente, *F. ochraceæ* typicæ valde affinis, sed sepalis multo latioribus corollâque albidâ distinguenda est.

Per habitum nanum, per flores fructûsque parvos inter Sectionis *Callianthos* species notabilis est, et alis petalorum interiorum bene explicatis albidis *R. erosam* in Sectione *Tripteryx* aliquanto refert.

Hæc varietas regionem montanam Djebel Antar, prope Mecheriam, in parte australi provinciæ Oranensis in Algeriâ habitat, ubi eam cl. Dr. Battandier anno 1888 collegit.

The description of this plant has been drawn up from material sent by the late Dr. Battandier shortly before his death, and the opportunity is taken of commemorating him in its name. Dr. Maire agrees that it is not identical with typical *R. ochracea*.

A form resembling this variety of *R. ochracea*, but apparently differing by narrower leaf-segments, capillary pedicels, and somewhat larger flowers with a remarkably developed spur, was collected by Joly in 1904 at Guelt-es-Stel, in the province of Algiers. The material seen is unfortunately insufficient for its accurate determination.

14. RUPICAPNOS GRACILIFLORA Pomel.

When the Revision was written no authentic material either of *R. africana* Lamk. or of *R. graciliflora* Pomel had been seen, and Lamarck's name was applied to the white-flowered species collected at Nedroma by Bourgeau (Pl. d'Alger. 1856, No. 184—cited in error as No. 181), which agreed more closely than any other material then examined with the descriptions of Lamarck and Desfontaines, and was at the same time evidently allied to *R. graciliflora* Pomel. A specimen of *Fumaria corymbosa*, sent by Desfontaines to the Museum at Copenhagen, has since been seen, which differs essentially from Bourgeau's plant and from Pomel's account of his *R. graciliflora*, and *R. africana*, which is the plant of Desfontaines and Lamarck, must consequently be treated as a separate species. Dr. Maire has been good enough to supply an authentic specimen of *R. graciliflora*, which, though differing in certain respects, is found to resemble the Nedroma form too closely to be specifically separated. A fresh diagnosis of *R. graciliflora* has therefore been drawn up from Pomel's material, and the Nedroma plant, which is larger, with less finely divided foliage and less rugose fruits, has been placed under it as a variety :—

*R. graciliflora* Pomel, Nouv. Mat. Fl. Atlant. i. 241 (1874) ; *Fumaria graciliflora* Batt. & Trabut, Fl. d'Alger. i. 25 (1888).

*Exsicc.* Pomel, Nador de Tiaret, 1860, in Hb. Alger. !

Rupicapnos perennis, caudice crassiusculo ut in *R. ochraceâ* caulibusque semper brevibus. *Folia* pleraque radicalia, 8–15 cm. longa (petiolo gracilescente incluso), *oblonga,* foliolis sæpius 3-paribus ambitu oblique ovatis breviter petiolatis et segmentis secundariis subflabellatis in *lacinias lineari-oblongas acutas* rarius mucronatas profunde et irregulariter fissis *2–3-pinnatisecta.* *Racemi* corymbiformes, 15–30-*flori*, cum pedunculo (ad 4 cm. longo) *foliis subduplo breviores.* *Bracteæ* 1·5–3 mm. longæ, *lanceolatæ*, tenuiter acuminatæ, parce denticulatæ ; *pedicelli fructiferi filiformes* apice paulo incrassati, *infimi ad* 30 *mm. longi.* *Sepala circa* 3 *mm. longa*, 2 *mm.*

*lata, ovato-lanceolata,* peltata, acuminata, *subintegra,* albida. *Corolla* 14–15 *mm. longa, gracilis,* carinis viridibus *albida*; *petalo superiore* apice marginibus paulo dilatatis subpatentibus vel deflexis sæpe leviter purpureo-tinctis *anguste oblongo obtuso, calcare longo* (ad 5 mm.) deflexo angusticollo apice rotundato; *petalo inferiore* marginibus patentibus angustis apice vix dilatatis *fere lineari, subacuto,* ad basin ipsam *plane saccato*; *petalis interioribus* apice sursum curvatis *modice alatis atropurpureis.* Stylus malleiformis. *Fructûs modici,* sine mucrone 2·5–2·75 mm. longi, 2 mm. lati, *oblongo-elliptici, cum mucrone brevissimo obtusissimi,* inferne breviter angustati, satis compressi et carinati, siccitate omnino *dense tuberculato-rugosi.*

β. *nedromensis,* var. nov.

*R. africana* Pugsley, Rev. Fum. & Rupicapnos, 343 (1919), ex maj. parte; non Pomel, nec *Fumaria africana* Lamk.

*Exsicc.* Bourgeau, Pl. d'Alger., 1856, Nedroma, in Hb. Mus. Paris (fructibus plerisque exclusis) et in herb. aliis (partim), ut *F. africana* !

*Folia* quam in typo *majora,* 10–25 cm. longa, *oblongo-deltoidea,* in lacinias oblongas vel lineari-oblongas fissa *2-pinnatisecta subquinata.* Racemi 15–20-flori; pedicelli fructiferi infimi ad 50 mm. longi. Sepala leviter dentata. *Corolla* paululum *major,* ad 16 mm. longa, petalis exterioribus apice magis dilatatis paulo obtusioribus, inferiore ad basin inconspicue gibboso-saccato. *Fructûs* obovato-elliptici, in sicco *tenuiter tuberculato-rugosi.* Aliter ut in typo.

*R. graciliflora* in rupibus dolomiticis ad Nador prope Tiaret in parte orientali, et varietas *nedromensis* ad Nedromam in parte occidentali provinciæ Oranensis Algeriæ crescit.

15. Rupicapnos platycentra Pomel.

The following description, taken from an authentic specimen kindly sent by Dr. Maire, is substituted for the incomplete account, adopted from Pomel, which appears at page 346 of the Revision.

*R. platycentra* Pomel, Nouv. Mat. Fl. Atlant. i. 242 (1874).

*Exsicc.* Pomel, Aïn Toucria, 1860, in Hb. Alger. !

Rupicapnos perennis, habitu *R. graciliforæ.* *Folia* pleraque subradicalia, ad 10 cm. longa (petiolo incluso), longe petiolata, *oblongo-deltoidea,* foliolis 2–3-paribus subdeltoideis et segmentis secundariis in *lacinias parvas oblongas* vel lanceolatas plus minusve acutas irregulariter et profunde incisis *2–3-pinnatisecta.* *Racemi* corymbiformes, 10–20-flori, cum pedunculo (ad 3 cm. longo) *foliis multo breviores.* *Bracteæ* 1–2 mm. longæ, *late oblongæ,* subacutæ, apice denticulatæ; *pedicelli fructiferi filiformes* apice incrassati, *infimi ad* 30 *mm. longi.* *Sepala circa* 2 *mm. longa,* 1·5 *mm. lata, suborbicularia,* peltata, acuta, *valde dentata* vel etiam basi laciniata, nervo viridiusculo albida. *Corolla magna,* 12–14 *mm. longa,* carinis viridiusculis *albida*; *petalo superiore* apice marginibus satis dilatatis patentibus vel deflexis *anguste*

*obovato obtuso, calcare magno*, 3·5–4 mm. longo, curvato, rotundato; *petalo inferiore* marginibus patentibus apice dilatatis *subspathulato obtuso* ad basin ipsam *obscure saccato*; *petalis interioribus* sursum curvatis *apice modice alatis atropurpureis. Fructûs magni*, sine mucrone 3 mm. longi, 2·5 mm. lati, *ovato-elliptici*, cum mucrone parvulo quadrangulato *acutiusculi*, satis compressi sed obscure carinati, siccitate omnino *grosse tuberculato-rugosi.*

Hæc planta, quæ a speciebus duabus precedentibus per corollam haud gracilem et per fructûs multo majores plane differt, *R. cerefoliæ* verisimiliter affinis est, sed habitu humiliore, bracteis latioribus, sepalis suborbicularibus, corolla minore, fructibus cum mucrone minore haud valde compressis facile separatur.

16. Rupicapnos cerefolia Pomel. (Pl. **17**.)

This beautiful *Rupicapnos* was seen in abundance on the rocks immediately below the little town of Milianah, and also less plentifully in a gorge on the mountain-side above. As is probably the case with the other perennial species of this Section, its fleshy stems, leaf-stalks and peduncles are remarkably brittle in the living plant, so much so indeed that, when carelessly grasped, a tuft readily breaks transversely into fragments in all directions. The mature plants generally become considerably branched, and the foliage is very glaucous, contrasting elegantly with the white and purple flowers. The racemes are generally very floriferous, sometimes bearing as many as thirty flowers. The white outer petals are frequently tinted with light purple towards the apex, while the purple tip of the inner petals has a short but rather broad dorsal wing, which sometimes is more or less white-edged, indicating a slight transition, less than that obtaining in *R. ochracea*, towards the form of inner petal characterising the Section *Tripteryx*. The style is clearly malleiform.

The fruits of *R. cerefolia* become much larger at maturity than those seen in the specimens from which the description in the Revision was taken. They are frequently 3–3·5 mm. long and 2·75–3 mm. broad, exclusive of the strong, quadrangular mucro, and are apically obtuse and strongly mucronate rather than acuminate. As indicated in the Revision, the fruit of *R. cerefolia* is more flattened and keeled than in the other species of this Section.

Seedlings of the first year were observed to be flowering at Milianah with the older and larger plants.

A form that seems referable to this species was collected by Dr. Maire in 1923 at El Hajeb, south of Meknes, in the Middle Atlas of Morocco.

### ** Series **Africanæ**.

Folia in segmenta pauciora majora vel satis lata tenuius fissa, vulgo petiolis crassis prædita. Flores albidi.

17. Rupicapnos speciosa Pomel.

The subjoined description has been drawn up from a co-type of Pomel's original gathering at the Cascade of the Mina in substitution for that in the Revision, which was chiefly based on the Saida plant at Kew. This latter plant appears to differ in its broader and more toothed sepals, and rather more shortly spurred corolla with a distinctly gibbous lower petal, and on these grounds should perhaps be held varietally separable. But in view of the imperfect material available it seems desirable to leave it at present undistinguished.

*R. speciosa* Pomel, Nouv. Mat. Fl. Atlant. i. 241 (1874).

*Exsicc.* Pomel, Mina prope Tiaret, 1860, in Hb. Alger. !

Rupicapnos perennis habitu *R. gracilifloræ* sed planta major. *Folia* pleraque subradicalia, ad 20 cm. longa (petiolo crassiusculo incluso), longe petiolata, *oblonga*, foliolis sæpissime 2-paribus subrhomboideis breviuscule petiolatis et segmentis secundariis flabellatis in *lobos oblongos obtusos* sæpe mucronatos irregulariter fissis 2-*pinnatisecta.* *Racemi* corymbiformes, *multi-* (circa 20-) *flori*, cum pedunculo ad 10 cm. longo *foliis paulo breviores. Bracteæ* 2–3 mm. longæ, *ovales*, cuspidatæ, parce dentatæ ; *pedicelli fructiferi filiformes* apice subito incrassati, *infimi ad* 30 *mm. longi. Sepala circa* 3 *mm. longa*, 2 *mm. lata, subrotundo-ovata*, peltata, acuta, basin versus *plus minusve dentata,* nervo dorsali viridiusculo albida. *Corolla magna*, 12–15 *mm. longa*, carinis viridibus *albida* ; *petalo superiore* marginibus apice paulo dilatatis subpatentibus purpurascentibus *fere oblongo obtuso, calcare modico* (4 mm. longo) curvato rotundato ; *petalo inferiore* marginibus patentibus apice paululum dilatatis *lineari-oblongo obtusiusculo, basi vix saccato*; *petalis interioribus* sursum curvatis apice *modice alatis atropurpureis. Fructûs majusculi*, sine mucrone circa 3 mm. longi, 2 mm. lati, *oblongo-elliptici, cum mucrone longo subacuti*, inferne parum angustati, valde compressi et plane carinati, siccitate omnino *dense tuberculato-rugosi.*

*R. speciosa* a speciebus precedentibus per folia majora minus dissecta plane differt.

18. Rupicapnos Mairei sp. nov. (Pl. **16**. fig. 6 b.)

*Exsicc.* Maire, Moulay Idris, 1923, in Hb. Alger. !

Rupicapnos perennis habitu *R. cerefoliæ. Folia* pleraque subradicalia, carnosa, glaucescentia, cum petiolo crasso laminam vix æquante ad 10 cm. longa, ambitu *anguste oblonga,* foliolis 3–4-paribus subdeltoideis (infimis breviter petiolatis, reliquis subsessilibus) et segmentis secundariis suboppositis in *lobos parvos oblongos mucronatos* subellipticosve irregulariter sed leviter fissis 2-*pinnatisecta. Racemi* corymbiformes, *multi-* (circa 20-) *flori,* cum pedunculo (ad 2·5 cm. longo) *foliis plane breviores. Bracteæ* 2–3 mm. longæ, *lanceolatæ*, acutæ, plus minusve dentatæ ; *pedicelli fructiferi graciles* apice incrassati, *infimi ad* 20 *mm. longi. Sepala* 2–2·5 *mm. longa et lata, orbicularia*

peltata, obtusiuscula, præsertim basin versus *inciso-dentata*, albida. *Corolla majuscula*, 11–13 *mm. longa*, *albida* vel leviter purpureo-tincta; *petalo superiore* marginibus apice parum dilatatis deflexis *anguste oblongo subacuto*, carinâ viridiusculâ petali apicem attingente, *calcare majusculo* 3–3·5 mm. longo rotundato curvato adscendente; *petalo inferiore* marginibus patentibus angustis apice haud dilatatis *lineari subacuto* ad basin *saccato*; *petalis interioribus* sursum curvatis *apice anguste alatis atropurpureis*. *Fructûs magni*, 3–3·25 mm. longi, circa 2·75 mm. lati, *subrotundo-obovati*, *cum mucrone brevissimo obtusissimi*, modice compressi sed plane carinati, siccitate omnino *grosse tuberculato-rugosi*.

*R. Mairei*, quæ inter affines per folia angusta breviter petiolata notabilis est, *R. speciosam* refert sed cum foliorum lobis minoribus, floribus calcare majore minoribus, fructibus multo majoribus obtusioribus humilior est.

Hæc species rupes calcareas ad Moulay Idris Mauritaniæ habitat, ubi a cl. Dr. Maire anno 1923 collecta est.

19. **Rupicapnos africana** Pugsley, Rev. Fum. & Rupicapnos, 343 (1919) partim, emend., non Pomel; *Fumaria africana* Lamk. Encycl. ii. 569 (1788); Coss. & Dur. in Bull. Soc. Bot. Fr. ii. 305 (1855), ex parte; Coss. Comp. Fl. Atlant. ii. 80 (1883–1887), ex parte; *F. corymbosa* Desfontaines in Act. Soc. Hist. Nat. Paris, i. 26 (1792), et Fl. Atlant. ii. 124 (1800), non Hammar.

*Icon.* Desfontaines, *l. c.* i. tab. 6, ut *F. corymbosa.*

*Exsicc.* Desfontaines, sine loco, in Hb. Haun., ut *F. corymbosa*! Maire, Iter Marocc. sept., Boulhaut, 1924, in Hb. Alger.!

Rupicapnos perennis, habitu *R. cerefoliæ* sed robustior. *Folia* pleraque radicalia, plus minusve glauca, carnosa, 10–25 cm. longa (petiolo crasso incluso), longissime petiolata, *oblongo-deltoidea*, foliolis 2-paribus subrhomboideis breviter petiolatis et segmentis secundariis subflabellatis in *lobos oblongos acutos* vel obtusos mucronatos irregulariter fissis 2-*pinnatisecta subquinata*. *Racemi* corymbiformes, *multi-*(15–30-) *flori*, cum pedunculo crasso (ad 6 cm. longo) *foliis subduplo breviores*. *Bracteæ* circa 2 mm. longæ, *ovatæ*, cuspidatæ, apicem versus dentatæ; *pedicelli fructiferi graciles*, apice incrassati; *infimi* 50 *mm. longi*. *Sepala* 2·5–3 *mm. longa*, 2 *mm. lata*, *deltoideo-ovata*, basi subtruncata, peltata, acuta, *valde dentata*, præter nervum dorsalem latum viridiusculum albida. *Corolla magna*, 13–15 *mm. longa*, vix gracilis, carinis viridiusculis *albida*; *petalo superiore* marginibus purpurascentibus apice vix dilatatis deflexis *anguste oblongo obtusiusculo*, *calcare breviusculo* (circa 3·5 mm. longo) rotundato deflexo; *petalo inferiore* marginibus patentibus apice vix dilatatis *lineari-oblongo subacuto* ad basin ipsam *gibboso-saccato*; *petalis interioribus* sursum curvatis *apice modice alatis atropurpureis*. Stylus malleiformis. *Fructûs magni*, sine mucrone 3–3·25 mm. longi, circa 2·75 mm. lati, *subrotundo-ovati*, *cum mucrone longo acutiusculi*,

inferne parum angustati, paulo compressi et satis carinati, siccitate omnino *grosse tuberculato-rugosi.*

Hæc species inter affines *R. speciosam* maxime refert, sed habitu robustiore foliis magis carnosis petiolis pedunculisque crassioribus fructibus majoribus minus compressis facile separanda est.

In rupibus prope Tlemcen et prope Mascaram provinciæ Oranensis in Algeriâ (apud Desfontaines) crescit, atque prope oppidum Boulhaut in parte occidentali Mauritaniæ, ubi a cl. Dr. Maire anno 1924 inventa est.

This plant, of which no authentic material had been seen when the Revision was written, is represented in the Herbarium at Copenhagen by a specimen sent by Desfontaines, which closely matches his descriptien and figure, and differs considerably from *R. graciliflora*, especially in its large, strongly rugose and long-mucronate fruits. It is therefore necessary to separate the two plants, and *R. africana* has now been described from Desfontaines' specimen and that recently obtained at Boulhaut, on the river Cherrat, in Western Morocco, by Dr. Maire. It may be expected that *R. africana* will be found in other Moroccan stations.

20. Rupicapnos decipiens Pugsley.

In Mémoires Soc. Scien. Nat. du Maroc, tom. iii. No. 1, p. 47 (1923), M. Jahandiez reports the occurrence of *Fumaria africana* Lamk. at Rabat and at Azrou in the Middle Atlas. Specimens from the former locality have not been seen, but there is a sheet from Azrou in Hb. Mus. Brit. which appears to be *R. decipiens β. mauritanica*, although both flowers and fruit are unfortunately missing. A specimen apparently of this variety, collected at Azrou in 1923, has also been received from Dr. Maire.

γ. *minor* var. nov.

*Exsicc.* Maire, Iter Marocc. dec., In urbe Taza, 16 juin, 1925, in Hb. Alger.! Maire, Iter Marocc. dec., Mahamran supra Taza, 17 juin, 1925, in Hb. Alger.!

*Planta* quam typus *minor*. *Folia* ad 8 cm. longa (petiolo incluso), quam in typo *magis dissecta,* foliolis in *lobos parvos* fissis 2–3-pinnatisecta. Bracteæ plus minusve dentatæ ; pedicelli fructiferi graciles apice incrassati infimi ad 40 mm. longi. *Sepala* præsertim basin versus *laciniato-dentata.* Corolla 12–14 mm. longa; petali superioris alæ nonnunquam sursum reflexæ. Fructûs typi sed paulo minores (ad 3 mm. longi). Aliter ut in typo.

Hæc Rupicapnos, quæ in duabus stationibus prope oppidum Tazam in Mauritaniâ septentrionali a cl. Dr. Maire inventa est, a speciebus Seriei *Cerefoliarum* per habitum magis carnosum, per petiolos pedunculosque crassiores et per foliorum lobos latiores quamvis parvos separatur.

The flowers and fruit of this Rupicapnos are scarcely distinguishable from those of the Spanish *R. decipiens,* of which it also possesses the very fleshy

habit, but it appears to be an essentially more dwarfed plant, with distinctly more dissected foliage.

### *** Series **Pomelianæ**.

Folia in segmenta lata relative magna leviter fissa, petiolis crassis prædita. Flores pallide purpurei.

22. RUPICAPNOS ORANENSIS Pugsley.

This species was collected by Admiral Lynes in 1923 at Jebela, West Spanish Morocco—a very notable westward extension of its range.

## SUBSECTIO **ANNUÆ**.

Plantæ annuæ, fragiles, haud carnosæ. Racemi pauciflori.

23. RUPICAPNOS GAETULA sp. nov.

*Fumaria africana* var. *gaetula* Maire in Bull. Soc. Hist. Nat. Afrique du Nord, ix. 172 (1918).

*Exsicc.* Maire, Djebel Grouz, 1918, in Hb. Alger. !

Rupicapnos radice longâ et caule nano (ad 10 cm. alto) vix ramoso haud crasso annua, raro perennans. *Folia* tenuia, pallide virentia, longissime petiolata, cum petiolo gracili ad 15 cm. longa, *oblongo-deltoidea*, foliolis sæpius 3-paribus infimis longiuscule petiolatis et segmentis secundariis in *lacinias* subflabellatas *oblongas subacutas* vel submucronatas irregulariter fissis *2-pinnatisecta*, vel primaria simpliciora. *Racemi* corymbiformes, *pauci-*(2–10-)*flori*, cum pedunculo brevi (ad 20 mm. longo) *foliis multo breviores. Bracteæ* ·5–1 mm. longæ, *lanceolatæ*, subintegræ, acutæ ; *pedicelli fructiferi filiformes* apice paulo incrassati *ad* 30 *mm. longi. Sepala parva*, 1·5 *mm. longa*, ·8 *mm. lata*, *ovata*, peltata, acuta, *dentata*, albida. *Corolla* 13–16 *mm. longa*, *gracillima*, *albida*, nonnunquam apice roseo-tincta ; *petalo superiore* marginibus apice parum dilatatis subpatentibus vel deflexis *anguste oblongo subacuto*, *calcare longissimo* (ad 5 mm.) curvato angusticollo apice rotundato ; *petalo inferiore* apice marginibus patentibus *subspathulato* subacuto *basi gibboso* ; *petalis interioribus apice* sursum curvatis modice alatis *purpureis*. Stylus malleiformis. *Fructûs mediocres*, sine mucrone circa 2·5 mm. longi et 2·25 mm. lati, *elliptico-rotundati*, *obtusiusculi et plane mucronati*, inferne in stipitem angustum contracti, paululum compressi sed valde carinati, siccitate omnino dense *tuberculato-rugosi*.

Hæc planta per radicem plerumque annuam, per habitum gracilem et per folia tenuia ab hujus Sectionis omnibus speciebus præcedentibus plane differt, et eorum caulibus carnosis foliisque crassis omnino caret. Sectionis *Muricaria* species corollis apice valde dilatatis fructibusque conspicue compressis longe distant.

*R. gaetula* in fissuris rupium calcarearum Djebel Grouz et Djebel el Maiz in regione Figuig Mauritaniæ austro-orientalis crescit, ubi a cl. Dr. Maire inventa est.

The description of this plant has been drawn up from a specimen kindly furnished by Dr. Maire, collated with his own detailed account.

### 24. RUPICAPNOS FRATERNA sp. nov.

*Fumaria* (*Rupicapnos*) *africana* Lamk. var. *fraterna* Maire in Hb. Alger. (nomen).

*Exsicc.* Battandier, Nemours, 1904, in Hb. Alger. !

Rupicapnos annua, radice longâ et caule haud carnoso suberecto (2–8 cm. alto) vix ramoso prædita. *Folia* haud crassa, longissime petiolata, cum petiolo 3–8 cm. longa, *deltoidea*, *foliolis* inæqualiter *subtrifidis* sæpius longiuscule petiolatis et segmentis secundariis in *lacinias* subflabellatas *lanceolatas acutas* mucronatasve irregulariter fissis *trisecta*. *Racemi* corymbiformes, *pauci-*(3–10-) *flori*, cum pedunculo ad 20 mm. longo *foliis multo breviores*. *Bracteæ* circa 1·5 mm. longæ, *ovales*, acutæ, subintegræ; *pedicelli fructiferi filiformes*, apice incrassati, *ad 25 mm. longi*. *Sepala parva, circa 1·5 mm. longa*, *·75 mm. lata*, *ovata*, vix peltata, acuta, *parce dentata*, albida. *Corolla* 9–11 *mm. longa*, verisimiliter *albida* plus minusve roseo-tincta; *petalo superiore* marginibus apice vix dilatatis subpatentibus vel deflexis *anguste oblongo subacuto, calcare breviusculo* (2·5–3·5 mm. longo) fere recto; *petalo inferiore* apice marginibus satis angustis patentibus *lineari subacuto ad basin,* ut videtur, *paululum gibboso*; *petalis interioribus* fere rectis *apice modice alatis purpureis*. *Fructûs mediocres,* sine mucrone 2·25–2·5 mm. longi, 2–2·25 mm. lati, *subrotundo-obovati*, *obtusi* et breviter *mucronati*, inferne multo angustati, parum compressi sed plane carinati, siccitate omnino *tuberculato-rugosi*.

Hæc *Rupicapnos* foliis trisectis, bracteis majoribus, corollis calcare breviusculo minoribus a *R. gaetulâ* satis differt; per folia trisecta *R. muricariam* simulat sed aliter omnino diversa est.

*R. fraterna* in fissuris rupium prope Nemours ad finem boreali-occidentalem provinciæ Oranensis in Algeriâ habitat, ubi cl. Dr. Battandier exemplaria anno 1904 collegit; apud Djorf de Taourirt in Mauritaniâ orientali probabiliter etiam crescit.

The description of this plant is founded on specimens from Nemours sent by the late Dr. Battandier as "*Rupicapnos* sp.," and by Dr. Maire as "*Fumaria* (*Rupicapnos*) *africana* var. *fraterna*," an unpublished name.

## EXPLANATION OF THE PLATES.

### Plate 15.

Fig. 1. Leaflet of *Fumaria atlantica* Coss. & Dur. *β. platyptera* Pugsley, with flower and fresh and dried fruits.
Fig. 1 a. Dried fruit of typical *F. atlantica* Coss. & Dur.
Fig. 1 b. ,, ,, *F. agraria* Lagasca.
Fig. 2. Leaflet of *F. rupestris* Boiss. & Reut., with flower and fresh and dried fruits.
Fig. 3. ,, ,, *F. mirabilis* Pugsley, ,, ,, ,,
Fig. 4. ,, ,, *F. major* Bad., *γ. algerica* Pugsley, ,, ,, ,,
Fig. 5. ,, ,, *F. Gaillardotii* Boissier, ,, ,, ,,
Fig. 6. ,, ,, *F. dubia* Pugsley, ,, ,, ,,

Leaflets all natural size; flowers and fruits × 2·5.

### Plate 16.

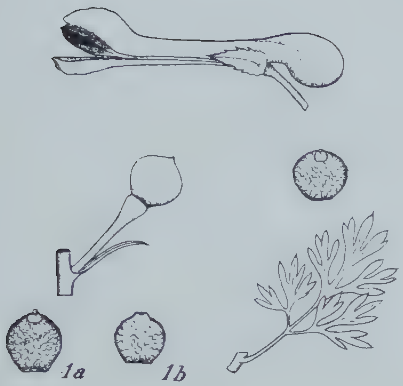
Fig. 1. Leaflet of *F. bicolor* Sommier, with flower and fresh and dried fruits.
Fig. 2. ,, ,, *F. maurorum* Maire, ,, ,, ,,
Fig. 3. Shoot of *F. algeriensis* Pugsley, ,, ,, ,,
Fig. 4. ,, ,, *F. Caroliana* Pugsley, ,, ,, ,,
Fig. 5. Leaflet of *F. ouezzanensis* Pugsley, ,, ,, ,,
Fig. 6 a. Flower and dried fruit of *Rupicapnos longipes* Pomel *β. elkantarica* Pugsley.
Fig. 6 b. Leaflet of *R. Mairei* Pugsley, with flower and dried fruit.

Shoots and leaflets all natural size; flowers and fruits × 2·5.

### Plate 17.

*Rupicapnos cerefolia* (natural size), with detached flower and dried fruit, × 2·5; drawn from a specimen collected at Milianah in 1922.

1



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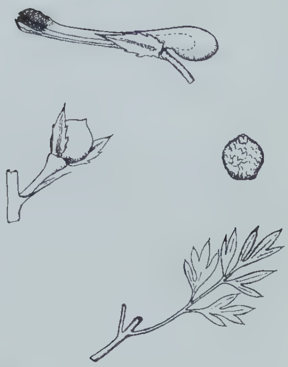

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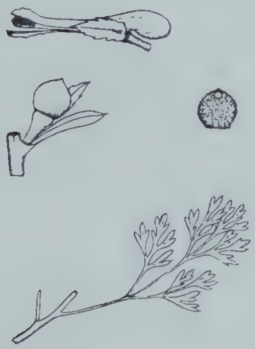

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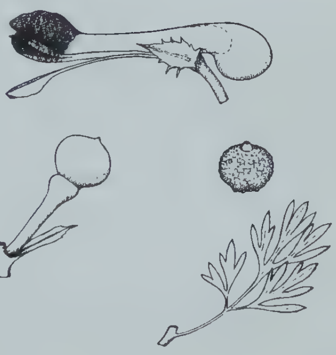

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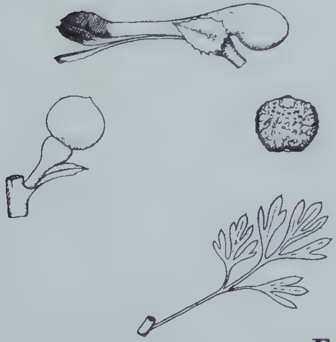

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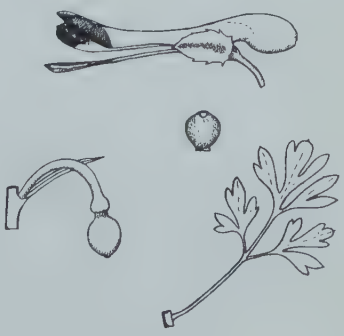
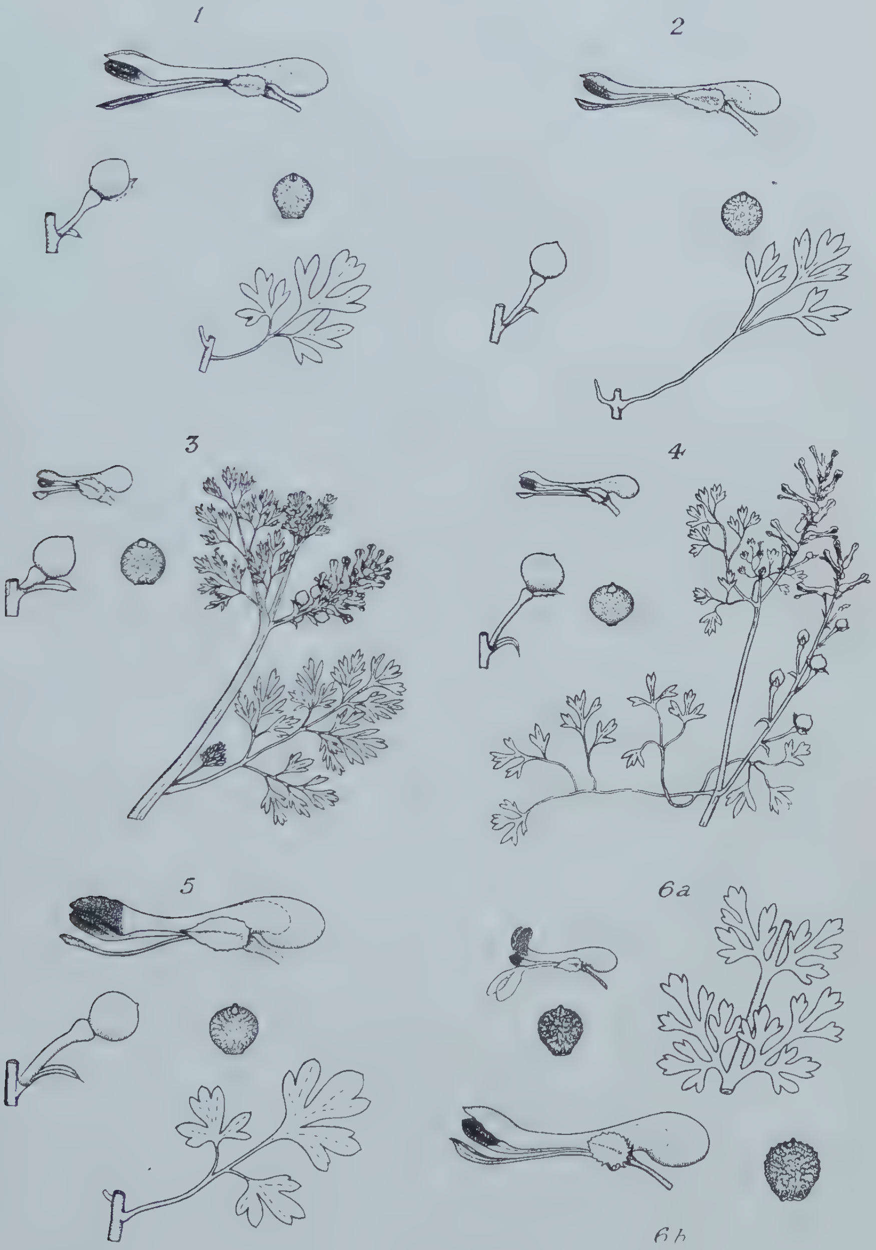
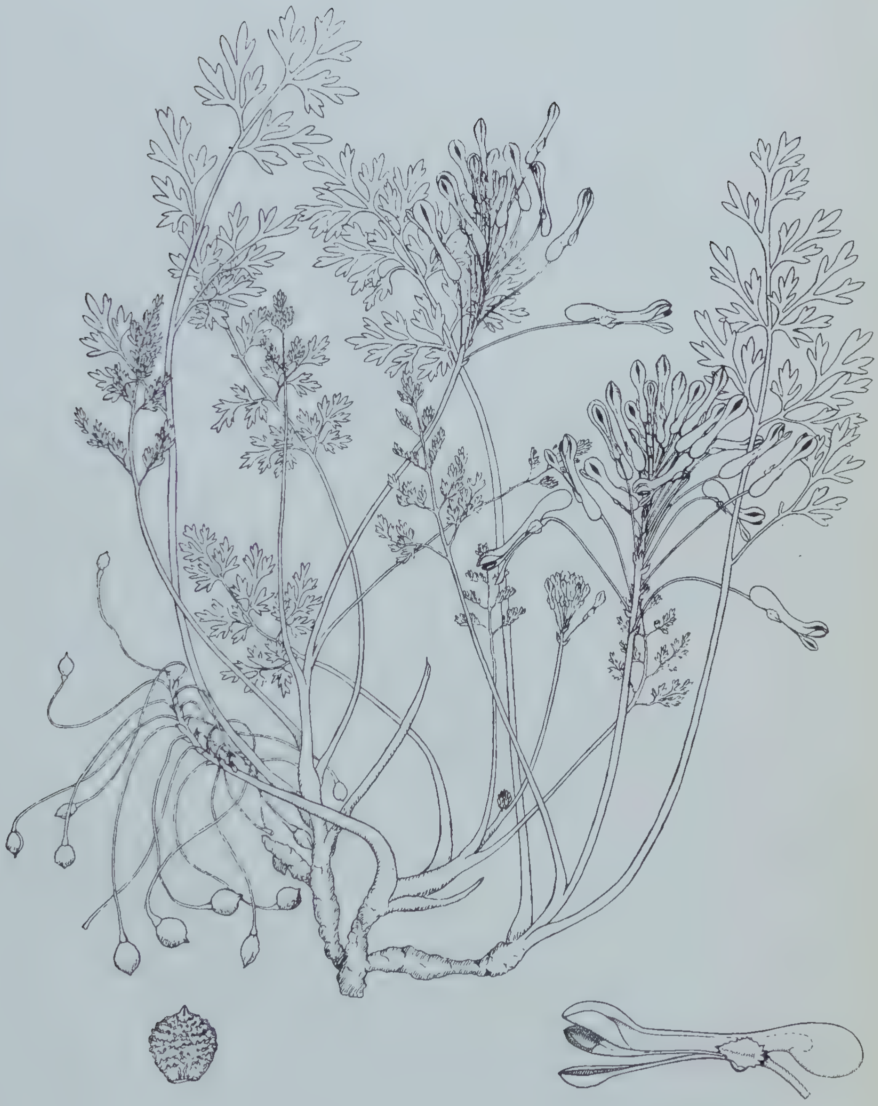


FUMARIA, *Linn.*



FUMARIA, *Linn.*



Rupicapnos cerefolia, *Pomel.*

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A star * denotes a name here published for the first time.

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# The Morphology and Taxonomic Position of the Adoxaceæ.

By T. A. Sprague, B.Sc., F.L.S.

(Plate 18.)

[Read 10th June, 1926.]

The Moschatel (*Adoxa Moschatellina* L.) has been known to botanists since the middle of the sixteenth century, and has repeatedly been the subject of investigation, yet numerous details of its morphology were still unknown at the beginning of the present century, and even now no adequate account of it exists in the English language.

The genus *Adoxa* has been assigned to Saxifragaceæ, Araliaceæ, and Caprifoliaceæ, and is now generally regarded as constituting an independent family, Adoxaceæ. This is placed by most modern authors next to the Caprifoliaceæ, but is considered by some to be related to the Saxifragaceæ or Araliaceæ. The taxonomic position assigned to Adoxaceæ is largely dependent on the morphological interpretation placed on the two floral envelopes. Wydler (**24**, **25**) regarded these as calyx and corolla, Eichler (**6**) as involucre and corolla, the calyx being suppressed, and Drude (**3**, **4**) as involucre and calyx, the corolla being absent. As the inner floral envelope is gamophyllous, those who accept Wydler's or Eichler's hypotheses place Adoxaceæ in the Gamopetalæ beside Caprifoliaceæ, whereas those who share Drude's views assign it to the Polypetalæ beside Saxifragaceæ or Araliaceæ. Before considering the arguments for and against the three hypotheses a condensed description of the Moschatel may be given. This has been drawn up mainly from Sturm's memoir (**23**), but contains various details from other sources, and some original observations.

## *General Description.*

*Seedling.*—By the growth of the embryo the endocarp is split into two flat valves. The short hypocotyl bears two cotyledons with long petioles and elliptic blades, emarginate at the apex and terminated by a hydathode. There is a single primary leaf, and the epicotyl develops directly into a rhizome.

*Rhizome* monopodial, at first filiform, bearing two rows of alternate scale-leaves, and expanding towards its apex into a slightly flattened bulb-like body. This bears 3–5 scale-leaves, 1–3 long-petioled foliage-leaves, and a single flowering shoot (less frequently 2–3 flowering shoots), and from its lower surface there arises a root. Branches of the rhizome originate in the axils of the scale-leaves.

*Foliage-leaves.*—Basal leaves long-petioled, once to three times, or even four times, tripartite or trilobed, very variable in size, but averaging about 8 cm. in length, exstipulate; each small lobe ends in a tooth 0·25 mm. long which terminates a vein and functions as a hydathode. A pair of similar but smaller leaves is borne above the middle of the peduncle; these cauline leaves frequently exhibit the phenomenon known as "doubling."

*Peduncle.*—This arises from the bulb-like expansion of the rhizome in the axil of a scale-leaf or foliage-leaf. It is usually about 8–10 cm. long and bears, above its middle, a pair of foliage-leaves (more rarely a single leaf), placed transversely with respect to the rhizome and the subtending leaf. The peduncle is tetragonal, and is divided into two parts by the pair of leaves. The lower part has four ribs at the angles, two running up into the midribs of the two leaves, and the other two at right angles, running up to the points of junction of the edges of the petioles. The upper part has its four faces vertically above the ribs of the lower, and each face has a median longitudinal groove. Sometimes, but rarely, secondary peduncles are produced in the axils of the cauline leaves.

*Inflorescence* (see Diagram IV).—The peduncle is terminated by a capitulum-like cyme, most frequently composed of five flowers, of which one is terminal, and the other four are in two decussating pairs, the lower pair being decussate with the pair of cauline leaves. Subtending bracts do not occur at the base of the pedicels of the lateral flowers. The order of expansion of the flowers is: (1) terminal flower; (2) lower pair; (3) upper pair. In each pair one flower expands before the other.

*Flowers* semi-epigynous, greenish, with an outer polyphyllous and an inner gamophyllous, rotate envelope bearing the stamens. In what follows these are provisionally termed the "outer perianth" and "inner perianth" respectively without any implication as to their true homology. The inner perianth is accrescent after dehiscence of the anthers. It falls off before the fruit is mature. The flower exhibits considerable meristic variation, especially in the inner perianth, andrœcium, and gynœcium. In typical inflorescences the parts of the flowers are as follows:—

*Lateral flowers* (see Diagram I).—Outer perianth trimerous, Y-shaped, two segments being obliquely posterior and the third anterior. Inner perianth pentamerous, with the odd lobe posterior. Stamens inserted on a raised ring at the mouth of the inner perianth, in five pairs alternating with its lobes; anthers monothecous. Carpels five, opposite the lobes of the inner perianth.

*Terminal flower* (see Diagrams II and III).—Outer perianth of two members, decussating with the upper pair of flowers, or more rarely of four members, the two additional ones being at right angles to the other two. According to Schumann (21), the primordia of the second pair are formed in all cases. Inner perianth tetramerous, the lobes placed diagonally with respect to the outer perianth. Pairs of stamens alternating with, and carpels opposite, the lobes of the inner perianth, as in the lateral flowers.

The inner perianth of the lateral flowers is slightly zygomorphic in consequence of the greater development of the posterior side of the flower, whereas that of the terminal flowers is actinomorphic.

*Æstivation.*—The æstivation of the outer perianth is open, and that of the inner perianth is imbricate. In the lateral flowers the æstivation of the inner perianth is quincuncial (see Diagram I), apotactous or paratactous *. In the terminal flower its æstivation is also imbricate, three different arrangements being exhibited: (1) two lobes wholly outside and two wholly inside (see Diagram II); (2) one lobe outside and one inside, not adjacent, the other two half-and-half; (3) one lobe outside and one inside, adjacent, the other two half-and-half (see Diagram III).

*Nectaries.*—At the base of each of the lobes of the inner perianth on its upper surface is a nectary composed of a group of about thirty minute glandular-capitate hairs.

*Andrœcium.*—Each pair of stamens arises from a single primordium, and is the result of actual division of a single stamen as in the Malvaceæ: hence the anthers are monothecous. They are borne on short filaments, and at the time of expansion of the flower are clearly, though obliquely, extrorse (see Diagrams I–III), although, according to Payer (**16**), they are introrse in their early stages.

*Gynœcium.*—Ovary syncarpous, semi-inferior, usually 5-locular in lateral, and 4-locular in terminal flowers. The carpels, however, are frequently anisomerous with the inner perianth lobes. Styles as many as the loculi and above them, free; stigmas at first punctiform, becoming more or less capitate at maturity. Ovules solitary in each loculus, pendulous, anatropous.

*Fruit* drupaceous, crowned by the segments of the outer perianth, containing five or four pyrenes about 3 mm. long, each surrounded by a slimy layer. Endocarp coriaceous, composed of two layers of fibres.

*Seed* albuminous, about 2 mm. long; endosperm copious, cartilaginous; embryo 0·3–0·5 mm. long.

### *The Homologies of the Outer and Inner Perianth.*

The available evidence is of two kinds: that derived from the normal or common types of inflorescence and flowers, and that obtained from the study of abnormal or rare types. While the latter category of evidence is often of the highest importance and cannot safely be disregarded, great caution is necessary in dealing with it, as many teratological phenomena are susceptible of two or more interpretations. The relative frequency of an abnormality, which can be ascertained only by the study of large numbers, may indicate whether it possesses any evolutionary significance, reversionary or progressive, or is merely what has been termed an "inconsequent" abnormality (22).

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* For the definitions of "apotactous" and "paratactous" see Riley, **19**. p. 210

The typical lateral flower of *Adoxa* may be considered first. *Prima facie* it appears to have neither subtending bract nor bracteoles, a condition which is parallelled in other genera and families. The trimerous outer and pentamerous inner perianth, however, taken together, are not suggestive of calyx and corolla: a corolla (in the absence of reduction) is usually either isomerous with its calyx or, less frequently, a multiple of it. Furthermore the odd sepal is usually posterior and the odd petal anterior, exceptions occurring in the Leguminosæ, *Lobelia*, *Rhododendron*, etc.

The hypothesis that the outer perianth represents the subtending bract of the flower and its two bracteoles explains the apparent absence of these members, the assumption being made that they have been carried up with the flower not only to the apex of its pedicel but half-way up the ovary. Examples occur of a bract and two bracteoles forming an involucre at the apex of a pedicel, *e.g.* in *Chrysosplenium* and Loranthaceæ, and, in view of what is now known of the ontogenetic development of an inferior ovary, the semi-epigynous position of the outer perianth does not preclude its being an involucre, though such a position is admittedly very unusual. The hypothesis also explains the orientation of the outer perianth with its odd member anterior, and the numerical ratio 3 : 5 of the outer and inner perianths, which would be anomalous for calyx and corolla. If the involucral nature of the outer perianth is accepted, then the inner perianth may be regarded as a calyx, as suggested by Drude. Eichler's view (1875) that it is a corolla involves the two assumptions that a calyx, of which no trace whatever remains, has disappeared, and that this hypothetical calyx had reversed orientation. It is simpler to regard the inner perianth as a calyx with normal orientation. On this view *Adoxa* is either primitively monochlamydeous, or, more probably, has lost its corolla. The "calyx and corolla" hypothesis of Wydler, accepted by Eichler in 1878, involves the three assumptions that the subtending bract and bracteoles of the lateral flower have been suppressed, that the orientation of calyx and corolla is the reverse of the usual, and that the calyx has suffered meristic reduction independently of the corolla. This explanation seems unnecessarily complicated.

The typical terminal flower of *Adoxa* is explained on Drude's hypothesis as comprising one pair (or two decussating pairs) of empty bracts and a calyx. On Wydler's hypothesis the numerical ratio 2 : 4 may be explained by meristic reduction of one member each in calyx and corolla from the 3 : 5 ratio found in lateral flowers.

Two salient characteristics of the inner perianth remain to be considered: (1) that it increases greatly in size after dehiscence of the anthers has taken place; (2) that it falls off before the fruit is mature. Its accrescent character is strongly in favour of its being a calyx rather than a corolla. Its deciduous nature might suggest *prima facie* that it was a corolla, but deciduous gamosepalous calyces bearing the stamens are not unknown, occurring for example in Rhamnaceæ and Thymelæaceæ, so that this character affords no evidence against the view that it is a calyx.

As regards typical flowers, it has been shown above that the "involucre and calyx" hypothesis of Drude is simpler and involves fewer assumptions than the "calyx and corolla" hypothesis of Wydler. The evidence afforded by abnormal and rarer types of flower may now be reviewed.

### *Abnormalities in the Inflorescence.*

Secondary flowering stems in the axils of the cauline leaves have been observed by Wydler, Sturm, and the writer. One or two additional flowers sometimes occur at the side or sides of the lateral flowers, apparently forming with them lateral 2–3-flowered cymes. One or two additional pairs of flowers may also occur above the usual two pairs. In view of the above facts Sturm's conclusion that the inflorescence of *Adoxa* has been reduced from a more compound condition will probably meet with general acceptance.

Wydler, A. Braun (**1**), and Sturm recorded the occurrence of one or two bracteoles (Vorblätter) on the pedicels of lateral flowers, and considered that this definitely disproved the involucre hypothesis of the outer perianth. Eichler in 1878 drew the same conclusion from the occurrence of one or two secondary flowers at the sides of the lateral flowers. *Prima facie* this conclusion might appear to be justified. When it is remembered, however, that the inflorescence of *Adoxa* is probably reduced, the lateral flowers with one or two bracts beneath them may be regarded as representing a reduced branch of the inflorescence, and the so-called "bracteoles" of the flower may really be the empty first bracts of this secondary axis. In that case the following dilemma might seem to arise. If the "lateral" flower is really terminal, it should have not a subtending bract and two bracteoles, but one or two pairs of empty bracts. This dilemma is more apparent than real. Many abnormalities are not susceptible of a simple morphological interpretation, but are to be regarded rather as the resultant of two or more conflicting tendencies. The classic example is the case of "double leaves," which are now generally interpreted neither as "forked" nor as "connate" leaves, but as structures intermediate between one leaf and two. In the present case the tendency to produce merely a lateral flower, and the tendency to produce a branch of the inflorescence with a terminal flower, have apparently resulted in the production of a flower of lateral type with 1–2 bracts or flowers beneath it.

Strong evidence in favour of the involucre hypothesis is afforded by the fact that the so-called bracteoles (Vorblätter) and the secondary flowers are mutually exclusive, and that subtending bracts (Tragblätter) and flowers on the main axis of the inflorescence are also mutually exclusive. The only explanation proffered by Sturm—that the crowded inflorescence leaves no room for the development of both subtending bract and axillary flower—does not seem adequate. Bracts are developed below the flowers in much denser inflorescences in other genera.

Sturm mentions five types of depauperate inflorescence as having been observed by him: 1, only the terminal flower developed; 2, terminal flower and a pair of empty bracts; 3, terminal flower, one empty bract and one lateral flower; 4, terminal flower and two lateral flowers; 5, terminal flower, upper tier composed of an empty bract and a flower, lower tier composed of two flowers. Similarly in luxuriant inflorescences he observed one or two additional tiers of flowers represented by (*a*) 1–2 empty bracts; (*b*) an empty bract and a flower; (*c*) 1–2 flowers. So far as Sturm's and the writer's observations go, the subtending bract and its flower never occur together. An adequate explanation of this is afforded by the involucre hypothesis: whenever a flower is developed in the axil of the bract it carries up the latter in its growth as the anterior member of the outer perianth, so that there is no subtending bract at the base of the pedicel. If this hypothesis of the "carrying up" of the bract is correct, intermediate stages might be expected to occur, in which the bract was carried only part of the way up the ovary; and Sturm himself admits that he observed "members of the calyx" in such extreme positions that it was not possible to say whether they were sepals, bracteoles, or subtending bracts. Under the heading "Teratologie" he mentions that one of the outer perianth segments is frequently inserted at a lower level on the ovary than the others, so that it is impossible to determine whether it is a bracteole or a perianth segment. Similarly in terminal flowers intermediate stages in the carrying up of the one or two pairs of empty bracts might be expected to occur. In a five-flowered inflorescence examined by the writer a third tier was represented by a pair of empty bracts, one of which was borne at the very base of the ovary of the terminal flower, while the other was attached to the ovary a short distance up. Another terminal flower had a tetramerous inner perianth and three superior outer segments, two being median and one transverse. A fourth segment, which may be interpreted as the missing transverse segment, was borne in an oblique position half-way up the ovary.

## *Correlation between Abnormalities of the Inflorescence and of the Terminal Flower.*

As already mentioned, the normal dimerous outer perianth of the terminal flower decussates with the upper of the two pairs of flowers usually present. When a third pair of flowers (or of empty bracts, or a pair consisting of a bract and a flower) is developed, then the outer perianth of the terminal flower decussates with that (see Diagram V). Sturm explains this correlation by there being more room available for the development of the outer perianth in the plane at right angles to the uppermost pair of lateral members. On the involucre hypothesis the outer perianth, being regarded as composed of a pair of bracts, will obviously decussate with the previous pair.

Perhaps the most significant example of correlation is when the additional tier is represented by a single bract or a single flower, the one opposite being apparently missing. In this case Sturm states that the outer perianth of the terminal flower is usually trimerous, one segment being diametrically opposite the single bract or flower, and the other two at right angles. He explains the gap in the outer perianth as being due to the formation of the additional flower below, which leaves no room for the development of the segment above it. The involucre hypothesis explains both the apparent suppression of one of the uppermost pair of bracts or flowers, and the appearance of an additional member of the outer perianth, by the carrying upwards of one of the bracts during the development of the ovary.

Out of five inflorescences possessing an additional tier represented by a single member (bract, flower or rudiment) examined by the writer, four had the terminal flower with a trimerous outer perianth, the extra segment being diametrically opposite the additional member; the fifth had the terminal flower with a dimerous perianth at right angles to the additional tier, which was represented by a bract. The absence of a third member of the outer perianth in this instance, as well as its presence in other cases where no extra flower is developed below the ovary, is doubtless due to the unequal development of the two flowers of each pair mentioned above under the heading "Inflorescence."

An extremely significant abnormality recorded by Eichler (**6**) was the occurrence of a terminal flower *without an outer perianth*. This terminated a 7-flowered inflorescence, and the absence of the outer perianth was attributed by Eichler to each of the two bracts of which it is usually composed having produced a flower in its axil, these flowers forming the third pair (see Diagram VI).

### *Abnormal Lateral Flowers.*

Out of 1555 lateral flowers examined by Sturm, 1462 (90 per cent.) had an outer perianth of the normal Y-shaped type, the other types represented ranging from five segments, the odd one being anterior, to one. According to Sturm, the meristic variation of the outer perianth is entirely independent of that of the other floral whorls—a circumstance which would suggest that it is an involucre rather than a calyx. In 100 inflorescences examined by the writer, 394 out of 412 lateral flowers, *i.e.* over 95 per cent., had a trimerous outer perianth. As regards the inner perianth, Sturm states merely that it is usually pentamerous, but frequently tetramerous or hexamerous. In the same 100 inflorescences examined by the writer, the inner perianth was pentamerous in about 85 per cent., tetramerous in 11·5 per cent., and hexamerous in 3 per cent. of the lateral flowers. Sturm gives tables showing the relative frequency of the various types of outer perianth in the 1555 lateral flowers examined by him. Apparently these were of different types as regards the inner perianth, a circumstance which unfortunately renders his percentages relatively valueless. It is curious that none of the eleven types of outer perianth figured by Sturm has a median posterior segment in view of the fact that such a segment occurs in nearly all lateral flowers with a diagonal tetramerous inner perianth, these diagonal flowers constituting about 25 per cent. of the total number of tetramerous flowers. Sturm appears to have interpreted all the median posterior segments seen by him as being oblique. He mentions that where there are only two segments of which one is anterior they usually lie practically in the same vertical plane, and that it is often difficult to decide whether the posterior one lies to the right or the left of the median plane. In the writer's experience abnormalities of the outer perianth are very rare in lateral flowers which are pentamerous as regards the inner perianth and andrœcium, and much more frequent in tetramerous and hexamerous lateral flowers. Certain common abnormalities in the position of the outer perianth segments in tetramerous lateral flowers are apparently correlated with the suppression of one of the members of the inner perianth, and a tetramerous outer perianth is certainly much more commonly associated with a tetramerous or hexamerous inner perianth than with a pentamerous one. These circumstances indicate that the variations of the outer perianth should be studied separately in flowers which are pentamerous, tetramerous, and hexamerous respectively as regards the inner perianth.

*Tetramerous Lateral Flowers.*—For the sake of brevity, flowers with a tetramerous (pentamerous, hexamerous, etc.) inner perianth are here termed "tetramerous (pentamerous, hexamerous, etc.) flowers," the members of the outer perianth are styled "segments," and the lobes of the inner perianth are referred to as "lobes." The results of an examination of 76 "tetramerous" lateral flowers were as follows. In 58 flowers (76 per cent.) the lobes were median and transverse, while in the remaining eighteen flowers (24 per cent.) they were diagonal. Of the 58 flowers with median and transverse lobes 56 had three segments, and only two had four segments. Out of the 56 flowers with three segments 54 had the odd segment obliquely anterior, instead of being in the median plane as in normal pentamerous flowers. The explanation here suggested is that in these 54 flowers the segments were laid down in the normal Y-shaped arrangement, but that, owing to the suppression of one of the two anterior lobes, a re-orientation took place, the two lateral lobes assuming a transverse position and the remaining anterior lobe assuming the median position, thus pushing the anterior segment on one side. The two exceptional examples in which the anterior segment was not displaced are illuminating. In both, two of the lobes occupied less than their normal half of the circumference of the flower, in one owing to their being smaller in size, and in the other owing to the suppression of the intervening pair of stamens. Thus these exceptions also can be explained by what may be termed the "re-orientation and displacement" hypothesis. Evidence which tends to confirm this hypothesis was afforded by two flowers which exhibited further abnormalities. In the one, although there were only four lobes, five pairs of stamens were present, two pairs being opposite the obliquely anterior segment, thus pointing to the suppression of a lobe on one side of that segment. In the other there were nine stamens instead of eight, three instead of two being opposite the obliquely anterior segment, the extra stamen indicating, as before, the suppression of a lobe. Furthermore, these three stamens were the youngest in the flower, thus suggesting that the obliquely anterior segment was really median in origin. As will be shown (p. 483) it is the anterior stamens which are normally the last to develop.

An alternative method of derivation of the "median and transverse" flower with oblique anterior segment is suggested by a flower in which the anterior lobe was bilobed, which might perhaps indicate that it had originated by the congenital union of the two anterior lobes.

Whereas 56 of the 58 "median and transverse" laterals form a homogeneous group, and have apparently arisen in one way—by the suppression of an anterior lobe and the consequent re-orientation of all the remaining lobes except the posterior, thus entailing lateral displacement of the anterior segment—the eighteen "diagonal" laterals seem to form a heterogeneous group, the diagonal position having apparently been attained in more than one way. Among the eighteen "diagonal" flowers, three principal types could be recognized : (1) six flowers had three segments so arranged that two were median and one transverse ; (2) five flowers had two segments in the median plane ; and (3) four flowers had four segments, median and transverse. It will be observed that a median posterior segment was present in each case. What is uncertain is whether the segment arose in that position or assumed it subsequently owing to displacement by the lobes of the inner perianth. Obviously many more examples must be studied before any conclusion can be reached as to the origin of these three types. The examination of 1000 tetramerous lateral flowers would probably afford sufficient data for generalisation.

*Hexamerous and Heptamerous Lateral Flowers.*—Hexamerous laterals apparently arise by the replacement of the posterior lobe by two lobes. Various intermediate conditions have been observed : (1) the posterior lobe may be merely bilobed ; (2) it is most frequently replaced by two lobes without an intermediate pair of stamens ; (3) occasionally a posterior pair of stamens is developed; and (4) very rarely, a posterior segment is also developed. Sturm interprets the additional pair of stamens as being one of a normally suppressed second whorl (see p. 483), but it seems simpler to regard the sixth segment, lobe and pair of stamens as being equally due to greater development of the posterior side of the flower, involving meristic increase in one or more whorls. A heptamerous lateral flower observed by the writer had evidently originated by the replacement of the posterior lobe and of one of the anterior lobes each by two lobes and an intervening pair of stamens. The three segments retained their normal Y position, and the stamens were thirteen, only a single one being present opposite the left posterior segment.

## *Abnormal Terminal Flowers.*

Sturm gives no idea of the meristic variation of the inner perianth in terminal flowers beyond stating that it is usually tetramerous, but very frequently pentamerous. Schumann found three pentamerous terminal flowers in about fifty inflorescences examined by him. In a hundred inflorescences examined by the writer the terminal flower was tetramerous (as regards the inner perianth) in 89 instances, pentamerous in nine, and trimerous in two. The 89 tetramerous inner perianths were associated with two outer segments in seventy instances, with three segments in fifteen, and with four segments in four. Thus 70 per cent. of the terminal flowers examined were typical as regards both outer and inner perianths. In the fifteen flowers having four lobes associated with three segments, the third segment was at right angles to the other two in fourteen, and oblique in the fifteenth owing to displacement due to one of the lobes being bilobed. In the four flowers having four lobes associated with four segments the latter were arranged in two decussating pairs.

Of the nine terminal flowers with a pentamerous inner perianth, five resembled typical lateral flowers in having three segments arranged in the shape of a Y, the odd segment decussating with the upper pair of flowers. A sixth flower was similar, but had an additional lateral segment ; it had five pairs of stamens and five styles. The remaining three flowers were more abnormal, and had apparently been modified from a tetramerous type by the appearance of an additional lobe. In two of them there were two segments decussating with the upper pair of flowers. The two segments had suffered little displacement or none, owing in one case to the crowding together of the three lobes on one side, and in the other to the absence of one pair of stamens on the 3-lobed half of the inner perianth. The third case was more complicated. The inflorescence was 5-flowered with a rudiment of a sixth flower above one of the lower flowers. The terminal flower had three segments, the space above the rudimentary flower being represented by a blank. Two of the segments were median and transverse respectively and the third was apparently transverse in origin, but had been displaced owing to the development of an additional lobe. Thus three out of the nine examples of "pentamerous" terminal flowers may be explained as modifications of the "tetramerous" plan. The origin of the remaining six examples is not obvious. On the involucre hypothesis two possible origins might be suggested: (1) that these flowers with three segments and five lobes have been derived by meristic increase from the normal terminal type with two segments and four lobes; (2) that the pentamerous terminal flowers are really lateral in origin, representing the only developed flower of an additional tier. Strong confirmation of the second hypothesis has been supplied by K. Schumann (21). Each of the three pentamerous terminal flowers observed by him occupied a markedly *oblique* position at an early stage of its development and—except for the anterior segment, which was the first to appear—each whorl developed in *descending succession.* Furthermore, the primordium of a sixth flower was present in each example at the back of the "terminal" flower. Schumann regarded the latter as being really terminal, and as owing its pentamery to the presence of the rudiment of the sixth flower acting as a "contact-body." He assumed that the lateral flower opposite the rudiment of the sixth flower had been suppressed. Schumann's hypothesis thus involved *three assumptions*: the suppression of a lateral (seventh) flower of the third tier; the oblique displacement of the terminal flower by the rudiment of the sixth flower; and the development of the "pentamerous" plan in the terminal flower owing to contact with this rudiment. On the other hand, the *single assumption* that the terminal flower has been suppressed affords a simple explanation both of the oblique position and of the pentamery of the apparent terminal flower. Schumann's explanation of the pentamerous terminal flower not only seems unnecessarily complicated, but is open to the further objection that it proves too much. If the presence of a sixth flower belonging to a third tier is sufficient to cause displacement of the terminal flower and alteration of its meristic plan from the "tetramerous" to the "pentamerous" condition, it should presumably always have this result, provided that no countervailing factors come into play, such as the retardation of the appearance or development of the sixth flower. But, as Sturm states, the appearance of a sixth flower belonging to a third tier is usually associated not with a pentamerous terminal flower, but with a tetramerous terminal flower in which the segment vertically above the sixth flower is suppressed.

If the pentamerous terminal flowers are really lateral in origin, the odd segment might be expected to be above the older flower of the lower pair, and to have the youngest anthers opposite it, as in a normal lateral flower. Besides the nine pentamerous terminal flowers mentioned above as having been examined by the writer, a few additional ones were seen, in some of which the segments were only two in number, one median and the other oblique. So far as the writer has observed, the median segment in pentamerous terminal flowers was above the older flower of the lower pair, but in the small number of examples seen it was not possible to determine the order of dehiscence of the stamens. Examination of about a hundred pentamerous terminal flowers at the appropriate stage of expansion would probably furnish sufficient data to test the "lateral origin" hypothesis.

As has been indicated above, in the hundred inflorescences examined two (*i. e.* 2 per cent.) of the terminal flowers had a trimerous inner perianth. Six trimerous terminal flowers in all were observed by the writer. Of these, only one had three segments arranged in the form of a Y; in the other five flowers there were two segments, one median and the other oblique. The median segment was above one of the lower pair of flowers, but it was not possible to ascertain whether it was above the older flower in all cases.

Although there is no direct correlation between the meristic increase or decrease of the outer perianth and that of the inner whorls, yet the number and position of the inner perianth lobes and the stamens appear to be to some extent dependent on the arrangement of the outer segments. Thus, in a lateral flower, the occurrence of a median posterior segment precludes the formation of a normal pentamerous inner perianth, and is usually associated with a diagonal tetramerous inner perianth. In the exceptional cases where it is associated with a pentamerous one the latter is asymmetrical.

### *Conclusions as to the nature of the Perianth derived from the study of Abnormal Inflorescences and Flowers.*

The evidence derived from abnormalities of the inflorescence and flowers is very greatly in favour of the "involucre and calyx" hypothesis.

(1) The mutually exclusive occurrence of "bracteoles" and secondary flowers. This necessarily follows from the "involucre and calyx" hypothesis. Sturm's suggestion that it is due to lack of space in which to develop does not seem to afford an adequate explanation.

(2) The mutually exclusive occurrence of subtending bracts and lateral flowers. The same remarks apply as in (1).

(3) The occurrence of segments in such a position that it is not possible to say whether they are subtending bracts, bracteoles, or outer perianth segments. This might be expected on the "involucre and calyx" hypothesis. On the "calyx and corolla" hypothesis it would have to be regarded as an "inconsequent" abnormality, which is improbable since, according to Sturm, it is one which frequently occurs.

(4) The occurrence of a gap in the outer perianth above a solitary flower of an extra tier. This would be expected on the "involucre and calyx" hypothesis. Sturm's "lack of space" explanation seems inadequate, as in (1) and (2).

(5) The want of correlation in the meristic increase or decrease of the outer perianth with that of the other whorls of the flower. This suggests that the outer perianth has had a different origin from the other whorls of the flower. If it were a calyx it might be expected to increase or decrease

along with the increase or decrease of corolla and andrœcium, but its meristic variation is frequently in the reverse direction.

(6) The occurrence of a terminal flower without an outer perianth (see Diagram VI). This is easily explained on the "involucre and calyx" hypothesis (see p. 477). On the "calyx and corolla" hypothesis it would have to be regarded as an "inconsequent" abnormality.

(7) The occurrence of 1–2 "bracteoles" or secondary flowers on the pedicel of a lateral flower. This has been considered by Wydler, A. Braun, Eichler (**7**), and Sturm as conclusive evidence against the "involucre and calyx" hypothesis, but, as indicated above (p. 475), it may be merely the resultant of two conflicting tendencies.

It will be observed that six out of the seven abnormalities lend strong support to the "involucre and calyx" hypothesis, and that the seventh does not constitute conclusive evidence against it.

### *Staminodes.*

According to Sturm, staminodes, undivided stamens or divided stamens sometimes occur opposite the lobes of the inner perianth in the same ring as the normal pairs of stamens. They exhibit all transitions from an undivided petaloid member to a perfectly developed pair of stamens, and Sturm had no doubt that they represented a normally suppressed second whorl of stamens. The possible taxonomic importance of this discovery is obvious.

### *Order of Dehiscence of the Anthers.*

It has already been mentioned that the posterior part of a typical lateral flower is more developed than the anterior, and that the "median and transverse" type of tetramerous lateral flower has probably originated by the suppression of one of the anterior lobes. Payer (**16**) observed, in correlation with the tendency to reduction of the anterior part of the lateral flower, that in each floral whorl the members developed in descending succession. Even the dehiscence of the anthers takes place in this order. The two posterior pairs of anthers dehisce first, then the lateral pairs, and lastly the anterior pair. Furthermore, in the posterior and lateral pairs, the posterior member of a pair dehisces before the anterior one, so that the anthers dehisce in five stages as indicated in Diagram I. The order of dehiscence in typical terminal flowers is rather irregular. According to Henslow (**10**) all the anthers dehisce simultaneously. According to Sturm, the anthers in the plane of the lower pair of flowers dehisce first, and then those in the plane of the upper pair. This is only partially correct. On the whole the anthers above the lower pair of flowers tend to dehisce first, but the first 1–2 anthers dehiscing may be above the upper pair, and the last 1–2 may be above the lower. An analysis of 48 flowers, in which 1–7 anthers had dehisced, gave the following results, L and U indicating respectively dehisced anthers above the lower and upper pairs:—1 anther dehisced (9 flowers), L 8 : U 1; 2 anthers (11 flowers), L 16 : U 6; 3 anthers (4 flowers), L 6 : U 6; 4 anthers (7 flowers), L 17 : U 11; 5 anthers (5 flowers), L 13 : U 12; 6 anthers (7 flowers), L 23 : U 19; 7 anthers (5 flowers), L 19 : U 16. Total 1–7 anthers (48 flowers), L 102 : U 71. As has been pointed out above, the order of dehiscence in pentamerous terminal flowers might shed light on their nature, as, if these flowers are really lateral in origin, the dehiscence of the anthers should take place in descending succession.

## *Geographical Distribution.*

*Adoxa* inhabits moist shady places, and has a circumpolar distribution in the north temperate zone, its area roughly coinciding with that of the northern forest region. In Europe it extends northwards to the Varanger Fjord, Norway (70° N.), the Kola Peninsula, and Kolguev Island; and its northern limit in Siberia is 70°–66° N. Its southern limits in Europe are the Pyrenees and the mountains of Avila (Spain), France, Corsica, Italy, Montenegro, N. Macedonia, N. Bulgaria, and Southern Russia. Apart from two apparently isolated areas in the Caucasus and Kashmir respectively, the southern limit of *Adoxa* in Asia appears to follow the Thian-Shan and Altai Mountains, Manchuria, Corea, and Japan. In America *Adoxa* extends southwards from the Arctic regions to New York, Wisconsin, Iowa, South Dakota and Colorado.

The Kashmir form of *Adoxa Moschatellina* has been described as var. *inodora* by C. B. Clarke (2), and is said to have 6-merous lateral and 5-merous terminal flowers. Two inflorescences have been examined by the writer. The lateral flowers had three outer segments arranged in the form of a Y and a 6-lobed (more rarely 5-lobed) inner perianth. One terminal flower had two outer segments in the same vertical plane, and the other flower had three outer segments, two being apparently in the same plane, and the third at right angles; in both flowers the inner perianth was pentamerous. Var. *inodora* has usually only one cauline leaf, more rarely two or none. Until it is better known, no certain conclusions can be drawn from the meristic characters of the flowers, but it seems significant that the pleiomery of the inner perianth is apparently not accompanied by any change in the number of outer segments. This want of meristic correlation is in favour of the "involucre and calyx" hypothesis.

## *The Taxonomic Position of the Adoxaceæ.*

As already mentioned, *Adoxa* has been considered to be related to Saxifragaceæ, Araliaceæ or Caprifoliaceæ, and a general review of its characters does not suggest a near relationship with any other family. The list of external characters which follows includes only such as appear to possess significance as pointing to a greater relationship with one or other of these three families. Each character is followed by the initial letter of the family or families which it suggests, greater or less community of character being indicated by the numerals (1), (2).

1. Herbaceous habit: (1) S. (2) In A. and C. herbs are rare.
2. Bulb-like expansions of the rhizome: S.
3. Alternate arrangement of the leaves on the rhizome: S., A.
4. Opposite arrangement of leaves on the peduncle: (1) C. (2) S.
5. Ternately divided foliage-leaves: (1) S., A. (2) In C. the leaves are usually undivided, but are pinnate in *Sambucus*, and lobed in some species of *Viburnum*.
6. Cymose inflorescence: S., C.
7. Carrying up of subtending bract and bracteoles: S.
8. Semi-epigynous flowers: S.
9. Gamosepalous calyx: S., C.
10. Apetaly: S.
11. Zygomorphy (of lateral flowers): (1) C. (2) S. (*Tetilla*, *Heuchera*, *Saxifraga*, *Tolmiea*).
12. Presence (as an abnormality) of a second whorl of stamens: S.
13. Bipartite stamens: S. These have been recorded as an abnormality in *Chrysosplenium* by Drude.
14. Extrorse anthers: C. (*Sambucus*).
15. Carpels usually as many as the sepals: (1) A. (2) C. (*Sambucus*, *Leycesteria*), S. (Hydrangeoideæ, Pterostemonoideæ).
16. Styles free: (1) S. (2) A., C.
17. Ovules solitary, pendulous: A., C.
18. Single integument: (1) A., C. (2) S. (Escallonioideæ, Hydrangeoideæ).
19. Drupaceous fruit: A., C.

A rough idea of the relative community of external characters between *Adoxa* and each of the three families may be gained by assigning five or three points respectively for greater or less agreement as regards each character. On this basis Saxifragaceæ comes first with 72 points, followed by Caprifoliaceæ with 52 and Araliaceæ with 38 points. The above analysis suggests that, if the Rosales, Umbelliferæ and Rubiales are accepted as representing natural groups, the Adoxaceæ should be placed in the Rosales–Saxifragineæ beside Saxifragaceæ. As has been seen, it has comparatively little in common with Araliaceæ, and its semi-epigynous apetalous flowers with distinct indications of the former presence of a second whorl of stamens seem sufficient to exclude it from the Rubiales.

Apart from the external characters the evidence in regard to the taxonomic relationships is conflicting. The anatomy of *Adoxa*, according to Morot (**13**), has more in common with Saxifragaceæ (especially *Chrysosplenium*) than with Caprifoliaceæ (*Sambucus*). Novak (**14**), however, considered that *Adoxa* did not exhibit much anatomical resemblance with *Chrysosplenium*, and Eichinger (**5**) stated that the two genera exhibited great dissimilarity in this respect. He laid stress on the different origin and arrangement of the stomata in *Adoxa*, the absence of tannin-sacs, and the absence of a well-developed central cylinder in the flowering stem. Hallier (**9**) considered that the anatomical features of *Adoxa* pointed to close relationship with *Sambucus*, and included the genus in the Caprifoliaceæ.

From a study of the developmental history and cytology of *Adoxa*, Lagerberg (**12**) concluded that a near relationship existed between it and *Sambucus*, but the very full comparison of these two genera given by Sturm reveals so many apparently important differences as regards other characters, that this conclusion can hardly be maintained. It receives some slight support, however, from the sero-diagnostic investigations of Raeder (**18**), who found that *Adoxa* serum gave strong positive reactions with Caprifoliaceæ (*Lonicera Xylosteum*), Dipsacaceæ (*Dipsacus silvestris*), and Rubiaceæ (*Sherardia arvensis*), and negative results with Saxifragaceæ (*Saxifraga aizoides*). Raeder's assumption that a comparatively close genetic relationship exists between *Adoxa* and the three families named appears to rest on sero-diagnostic experiments on a *single* species of each family, which is hardly an adequate basis.

A possible explanation of the apparent double relationship of *Adoxa* with the Saxifragaceæ on the one hand and the Caprifoliaceæ on the other may be that the Rubiales and the related Umbellifloræ have descended from forms allied to the Rosales. But hypotheses of this nature belong as yet to the realm of pure speculation, and are useful only in so far as they stimulate the employment of additional characters in taxonomic work and thus promote the acceptance of a wider basis of classification.

In conclusion the writer desires to thank Mr. W. B. Turrill for various bibliographical references and for data regarding the distribution of *Adoxa* in the Balkan Peninsula.

## EXPLANATION OF DIAGRAMS. (PLATE 18.)

I. Theoretical diagram of typical lateral flower of *Adoxa Moschatellina*: *a*, axis of inflorescence; *s.b.*, subtending bract; *α*, *β*, bracteoles, these and the subtending bract forming the "outer segments"; *s*, *s*, sepals ("inner perianth-leaves"); anthers numbered 1–5 in order of dehiscence.

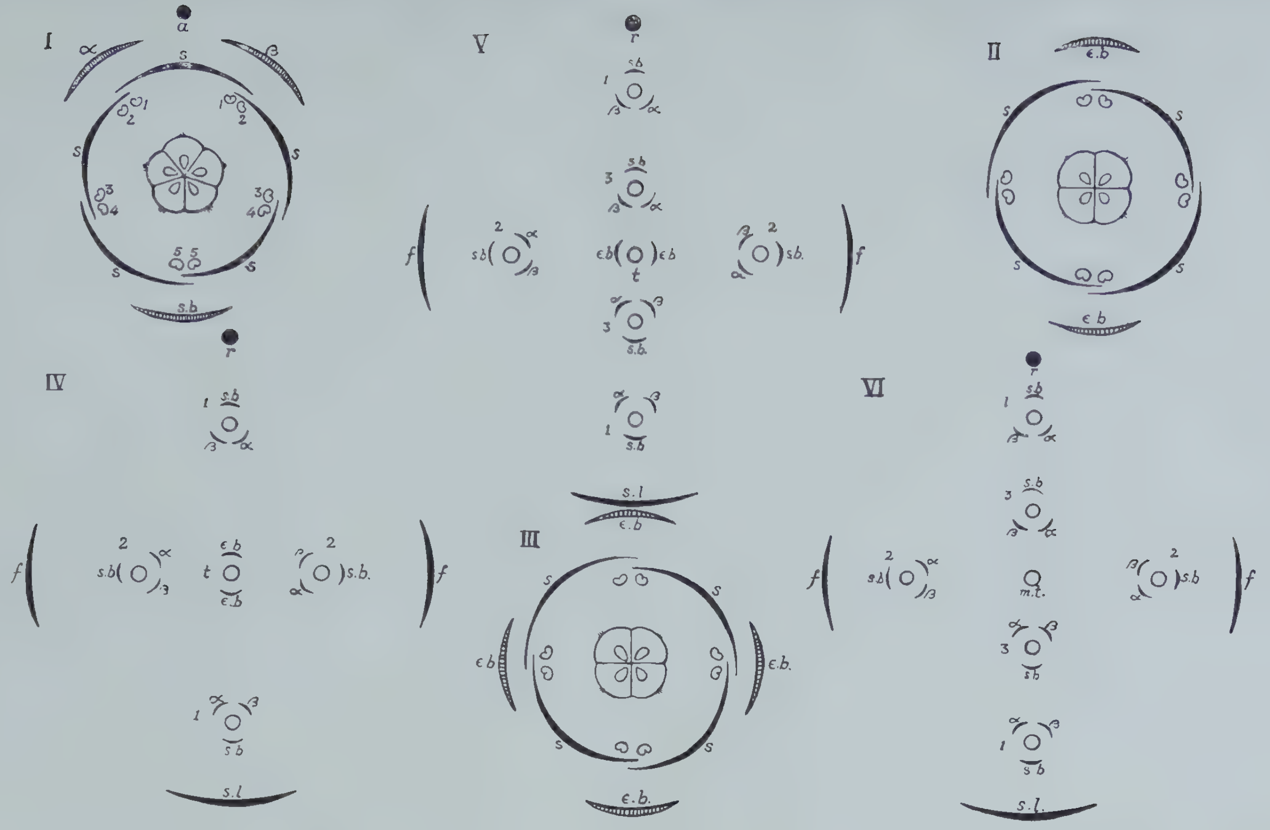
II. Typical terminal flower with 2 "outer segments": *e.b.*, empty bracts ("outer segments"); *s*, *s*, sepals ("inner perianth-leaves").

III. Terminal flower with 4 "outer segments"; lettering as in II.

IV. Ground-plan of typical 5-flowered inflorescence: *r*, axis of rhizome; *s.l.*, subtending leaf; *f*, *f*, cauline leaves; 1, 1 and 2, 2, first and second pairs of lateral flowers; *s.b.*, subtending bract; *a*, *β*, bracteoles; *t*, terminal flower; *e.b.*, empty bracts.

V. Ground-plan of 7-flowered inflorescence: 3, third pair of lateral flowers; remainder of lettering as in IV.

VI. Ground-plan of 7-flowered inflorescence with a terminal flower without an "outer perianth": *m.t.*, "monochlamydeous" terminal flower.



ADOXA MOSCHATELLINA L.

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## The Genus *Empetrum* L. By R. D'O. Good, M.A., F.L.S.

(With 4 Text-figures.)

[Read 6th May, 1926.]

One of the chief difficulties confronting the taxonomic botanist is his necessarily imperfect knowledge of the plants with which he has to deal. In many cases whole minor plant groups are known, to European botanists, only from a small number of incomplete dried specimens. The result of this is that in taxonomic botany a certain method of procedure has arisen, and certain valuations of criteria have developed which of necessity are more or less artificial and without any strictly scientific foundation. In such circumstances it is only by analogy with other better-known plants that the nature of the lacking information can be suggested. It was therefore thought that a useful purpose might be served by the careful and detailed description of the variation and geographical segregation seen in a small and well-known group of plants, and by suggesting a taxonomic treatment in accordance with the facts. The most convenient unit for such a purpose is the genus, but the genus selected should have several special features: great abundance, so that an extensive series of specimens may be available for comparative study; a very wide geographical range, preferably discontinuous; a conveniently small size so as to avoid too great complexity, and, finally, a well-defined morphology so that there can be no question as to its exact limits. All these requirements are fulfilled in the genus *Empetrum*, a genus familiar to most British botanists because it contains the Black Crowberry, so important a feature of the vegetation of the Yorkshire grouse moors.

### The Family EMPETRACEÆ.

The family Empetraceæ (**4**, **30**) consists of three small genera, *Empetrum*, *Corema*, and *Ceratiola*. All are small shrubs of ericoid habit with numerous, small, close-set, acicular leaves, inconspicuous, normally unisexual flowers and drupaceous fruits. The systematic position of the family has always been a subject of discussion and is by no means certain. By de Jussieu (**22**), Agardh (**1**), Gray (**16**), Baillon (**3**), Solms-Laubach (**38**), and Hallier (**18**) it has been considered to show most affinity with the Ericales, by Nuttall (**29**) it was placed nearest the Coniferæ, by Le Maout and Decaisne (**24**) near the Ilicineæ, while Don (**8**) and de Candolle (**5**) emphasized its resemblances to the Euphorbiaceæ. More recently Bentham and Hooker (**4**) have treated it as an anomalous order, Pax (**30**) as a part of the Sapindales, Warming (**39**) as belonging to the Tricoccæ, and Wettstein (**40**) as among the Celastrales. The whole question has been carefully considered by Gunnar Samuelsson (**32**) who concludes that it must certainly be placed in the Ericaceæ, preferably as a fifth group after the Ericineæ. The consensus of opinion also accords with this view, which is supported by such characters as the lack of an endothecium in the anthers, the production of tetrad pollen, the development of the seed, the single-layered epidermal testa, and the way in which the endosperm is formed. Two other facts afford somewhat different evidence for the same opinion. A genus of fungal parasites, *Chrysomyxa,* is particularly characteristic of the Ericaceæ in the range of its host plants. It contains sixteen species of which thirteen affect plants belonging to this family. One species is found exclusively upon *Empetrum.*[*] Secondly, *Empetrum* has been shown by van Itallie (**21**) to contain urson, a chemical compound found elsewhere only in some of the Ericaceæ.

## THE GENUS EMPETRUM.

*Empetrum* is a genus of small heath-like shrubs, with many small acicular, shortly petiolate, entire leaves, generally in a close-set spiral arrangement. These leaves have a peculiar structure, well described by Gebelli (**14**). Down the ventral or abaxial surface is a narrow slit, fringed with long hairs, and opening into a cavity in which the stomata are situated. The lips of the slit appear to be formed by the reflexed leaf-edges as in typical ericoid foliage, but actually the apparent leaf-edges are the true leaf-edges and the cavity below arises by the formation and subsequent enlargement of a deep sulcus on the under side of the thickened tip of the young leaf.

The flowers are borne singly on very short shoots in the axils of the upper leaves. Each of these shoots bears three bracts, which show by their arrangement that the single flower is the remnant of a three-flowered cyme. Very rarely more than one flower may be developed. The flowers are normally unisexual and have 2 or 3 free sepals, imbricate in bud, and 2 or 3 persistent, free petals. In the male there are 3 or 4 stamens with 2-celled, deciduous anthers and long filiform, persistent filaments: in the female there are minute staminodes, and a superior 3–9-celled ovary with a short style and a 6–9-branched stigma. The fruit is a fleshy drupe with 1–9 one-seeded stones. The seeds have a thin testa, fleshy albumen and a straight embryo.

Flowering takes place in March or April, or later according to latitude, and pollination is by wind (although the stigmas have been said to secrete honey). The fruits are eaten by birds and other animals and are apparently dispersed by them, but the seeds do not germinate readily and most reproduction is vegetative.

The plants may live for many years and as many as one hundred and forty annual rings have been counted in a stem from Norway. The foliage buds are protected by deciduous bud-scales. Vernal shoot growth begins shortly after flowering but soon stops; summer shoots begin to grow in June. Schroeter (**33**) states that the plant has an endotrophic mycorrhiza. The fruits are palatable and are used in various ways in many parts of the world. The plant also affords a valuable fuel.

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[*] The other two are known only in the teleutospore stages on *Picea.* The æcidiospore stages of some of the other species are also found on *Picea.*

## Geographical Distribution.

*Empetrum* has a geographical range which is not exactly paralleled by that of any other Angiosperm. This includes the cooler temperate parts of both hemispheres, but is, as far as is known, without any intermediate stations in the subtropics or tropics. Its distribution in the north is completely circumpolar: in the south it inhabits part of the American continent, the Falkland Islands, and the Tristan da Cunha island group.

In the Northern Hemisphere its northern limit is that of the flowering plants as a whole, and it has been collected from a number of localities above the latitude 80° N. It is to be found, often plentifully, on most of the islands of the Arctic-American Archipelago and is a common plant apparently almost throughout the coasts of Greenland, especially on the western side. On the American continent its southern limit varies considerably. In the west it extends down through Alaska and along the granitic coast-ranges to British Columbia and Vancouver Island. It occurs in isolated localities on rocks and mountains as far south as northern California. It is said to be absent from the main range of the Rocky Mountains, but this is very doubtful, and it is certainly a fairly common plant in the Canadian Rockies of the Lake Louise district at altitudes up to 7000 ft. Eastward of the mountains its southern border is much farther north, following the junction between the sub-arctic forests and the prairies. Towards the east coast it again extends south to the northern shores of Lake Superior and Georgian Bay, whence it crosses to Montreal and the St. Lawrence. North of the river it is very common throughout Quebec and Labrador, but south of the river it is found only in isolated localities on the mountains of Maine and New Hampshire and in bogs and on coastal rocks throughout Nova Scotia. It is abundant on Newfoundland and on Anticosti. Taylor has reported it at sea-level on Long Island at a latitude of 41° N., and this appears to be its extreme southern limit on the eastern coast *.

In the Northern Old World *Empetrum* is again found as far north as any Angiosperms and is well known from Spitzbergen, although it but rarely flowers or fruits there. It is also plentiful in Iceland, but has not been recorded from Jan Mayen. Similarly, while abundant on the islands just off the north European coast it is extremely rare on the mainland of Novaya Zemlya. In Great Britain it is found almost everywhere in suitable

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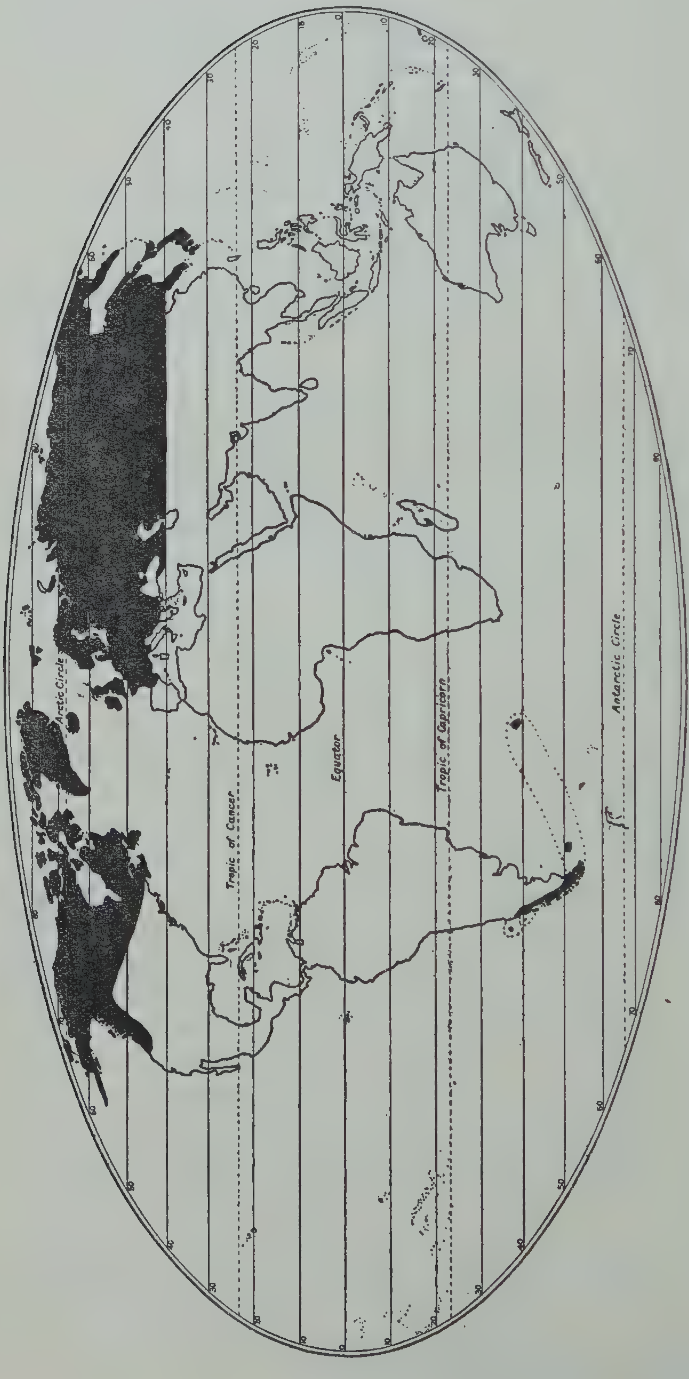
* There is a specimen in Herb. Berlin labelled "Florida," but in absence of confirmatory data this locality cannot be accepted as authentic.

Fig. 1.



Distribution of the genus Empetrum and of the species E. nigrum L. (Northern Hemisphere).

localities, from sea-level on the south coast to the summits of Highland Mountains. On the Eurasian continent its south-western limit is reached in the Pyrenees and on the mountains of Catalonia and Arragon. It is common throughout central and northern Europe and just reaches the northern Apennines in Italy. There are several records for it in the Balkans (Bulgaria and Montenegro). East of the Black Sea it is a well-known plant in the Caucasus, and in the north-east of Asia Minor extends as far west as 38° E. In continental Asia the records of its occurrences are meagre, but as far as is known, its southern limit across the continent is about the latitude of 40° N. It is known also from the Urals and the Altai and from various places on the Arctic coast as well as from some of the Siberian islands. Farther east the data begin to be more plentiful again. Here its limit skirts the northern edge of the great continental desert and extends south once more in Mongolia. The plant is common in Amurland and Korea and there are records for it all over Kamchatka, the Kuriles, Saghalien and Japan, but in the latter at any rate it does not seem to be a very common or conspicuous plant. It does not occur in China or in the great Himalayan mountain system.

In short, in the Northern Hemisphere, *Empetrum* may be said to be practically ubiquitous above the latitude of 40° N.

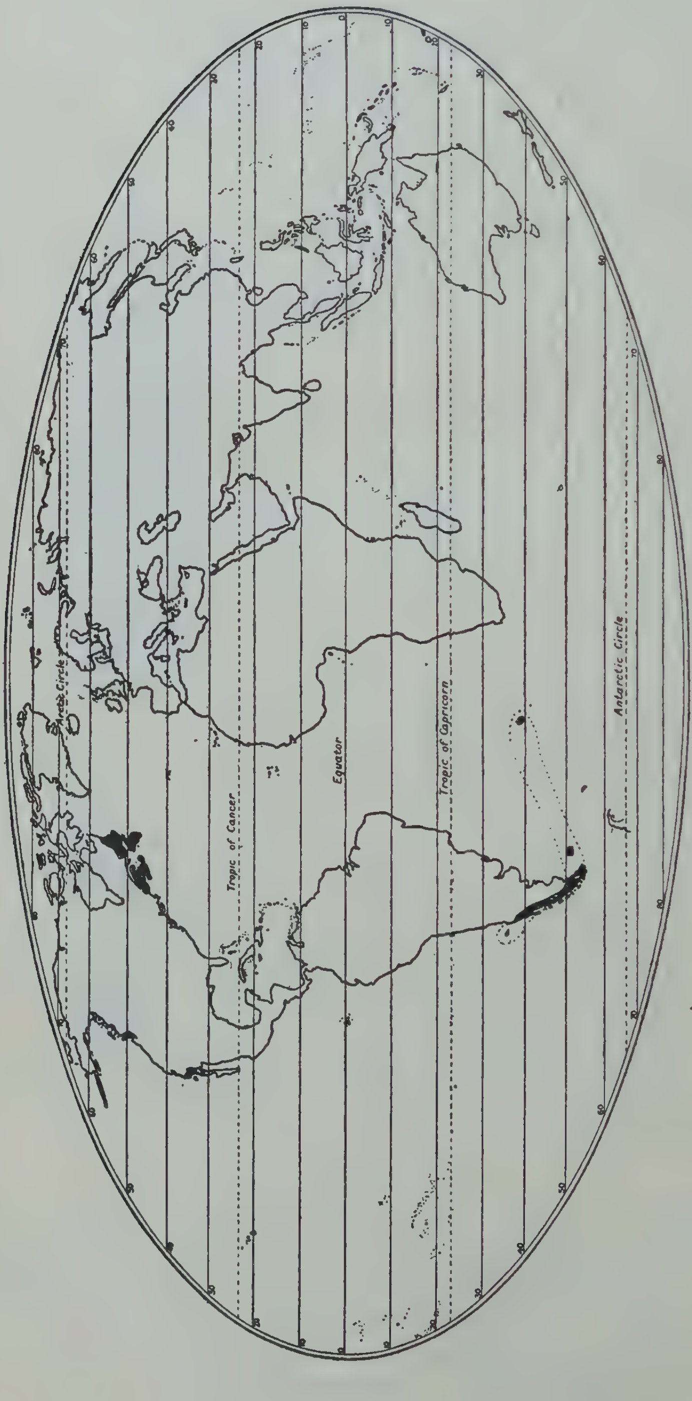
The range of *Empetrum* in the Southern Hemisphere is much more restricted. It is found commonly along the western coast of the South American continent southwards from the latitude of Concepcion and Mendoza, but its actual extreme northern limit is on the island of Masafuera in the Juan Fernandez group, where Skottsberg (**37**) found a single very old plant on the summit of a mountain. It does not appear to cross the Andes or to be found in the Argentine. Farther south, in Fuegia, it is found everywhere from west to east and extends into southern Patagonia. South-east of the continent it is very abundant in the Falkland Islands, but has not been reported from South Georgia or the Antarctic continent. Finally, at a distance of nearly 2500 miles from the Falklands, *Empetrum* is very plentiful and occurs on all the islands of the Tristan da Cunha group, where it forms one of the most conspicuous elements in the flora.

It may be noted that *Empetrum* is not found at all in Australasia, even in those parts having a similar latitude to that of southern Chile.

## ECOLOGY.

Throughout its range *Empetrum* is found in four main, and more or less, distinct types of habitat: peat bogs, bare rocky places, sands and heathlands. It is practically unknown from calcareous rocks and soils but abounds where potassium is plentiful (Fernald, **11**). These habitats vary slightly in character from one part of the generic range to another, but all resemble one another in the lack of mineral salts, especially calcium, and in the deficiency

FIG. 2.



Distribution of Empetrum rubrum Vahl.

of nitrogen in available form. The plants require much light and air and so are found only in the most open kinds of woods. Like many other heath plants, they seem able to grow in either very wet or dry soils.

## Variation.

When a long series of *Empetrum* specimens is examined, it is at once evident that there is a considerable amount of intra-generic difference between the individuals and that these differences are due to variation in certain definite morphological characters. Investigation shows that the characters chiefly concerned are very few in number, only seven being sufficiently important to be considered at length. A number of others can be detected easily, but the variation in these does not play a large part in the external differences between individual plants.

The seven important characters are :—

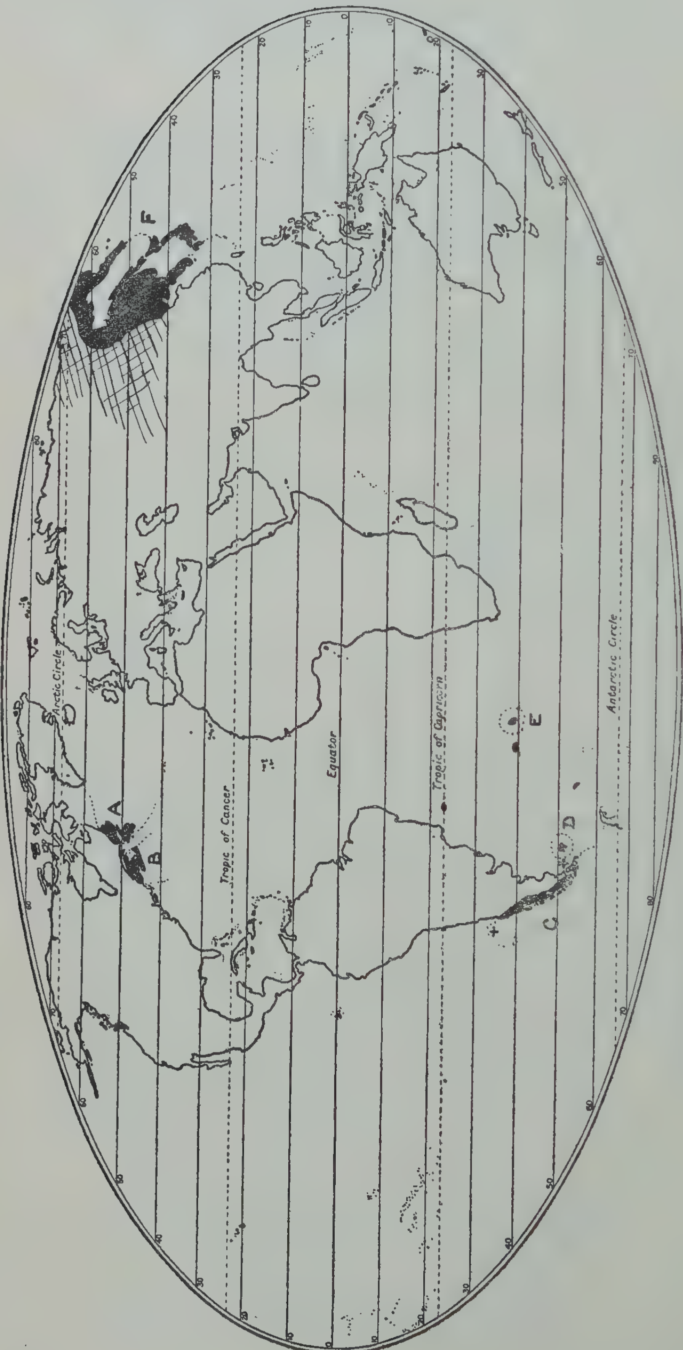
1. General habit.
2. Degree of hairiness.
3. Shape and size of leaf.
4. Arrangement of leaves.
5. Angle of leaf-insertion.
6. Sex of flowers.
7. Colour of berry.

### 1. *General Habit.*

Variation in general habit is the chief cause of the most obvious differences in form between individual plants. Such difference in habit is due to variation in two directions, namely, strength and structure of the various axes and in the number and length proportions of the branches. Vegetative growth in *Empetrum* occurs in two stages, and as a result there are both spring and summer shoots. Growth in the main axis is chiefly due to the former. In the most general terms there are three main habit forms.

First : straggling procumbent habit in which the main axes are developed far more than the lateral branches although these latter may be very numerous. This form may be looked upon as the most general and is certainly the most widely distributed, especially over the Northern Hemisphere. Its most marked condition is seen in plants growing near sea-level in sandy or heathy places, as in the south of England. In these the growth increments are long and the main axis stout, while the laterals are fairly long and not very closely set. The whole plant is procumbent but the ends of the branches tend to become erect. The prostrate main axis produces roots on the under side so that the plant becomes truly creeping. The lateral shoots are shorter than the main axis and are produced in groups at wide intervals. Farther north and in various places in the south where vegetative conditions are not so good, the growth increments tend to be shortened and

Fig. 3.



Distribution of :—

**A.** E. rubrum v. Eamesii, ++ possible Southern records.
**B.** E. ,, v. atropurpureum.
**F.** E. nigrum f. japonicum.
**C.** E. rubrum f. andinum.
**D.** E. ,, f. falklandicum.
**E.** E. ,, f. medium.

the plant, while still procumbent, is much more closely built, smaller and less straggling.

Second: a much more compact plant in which the main axis is to a great extent shortened and upright and the lateral branches are also more equally developed and erect, lying fairly close to the main axis. The result is a small bushy plant with ascending branches. This bushy form must not be confused with the compact but still procumbent Arctic form mentioned above, and the bushy appearance is certainly due to a difference in internal anatomical structure. This form is apparently common in Japan and Kamchatka, but is also found in alpine situations such as the Alps and southern Canadian Rockies. Different as the form is from the procumbent one there is no actual demarcation between the two and there is a long series of intermediate forms, probably owing to a varied development of anatomical features. As would be expected, the main stem towards the ground level may become large, up to 1 cm. in diameter, and sections have shown that it may contain as many as 150 growth-rings. In the typical procumbent form the older portions do not persist so long, and fresh centres of attachment to the soil are formed from time to time.

Third: the true cushion form. Several features go to the production of this form. The branches tend to be somewhat gnarled and twisted, the laterals lie at a more widely divergent angle than in the bushy form, the growth increments are equalized and small, and the main axis is frequently branched. Correlated with the cushion habit is the early loss of the lower leaves and the close accumulation of the living ones at the tips of the branches. Similarly the flowers also are massed at the tips. This true cushion habit shows a very restricted geographical range and is entirely confined, in any case in its fullest expression, to the Southern Hemisphere. Here it is seen at its best and to the exclusion of other forms, in the Falkland Islands, where the plant sometimes attains quite a large size and may be several feet in diameter. As might be expected the stems are sometimes very large, and in Herb. Kew there is a specimen with the pencilled note "with stems 6 inches across." This statement cannot be accepted without question, but it may well be true. The cushion form seems to be most closely allied to the procumbent one, and many plants show an intermediate character. The bushy form seems to be a divergence in another direction.

A minor but conspicuous growth-form occurring among the plants of Tristan da Cunha may be mentioned here. It seems to be intermediate between the procumbent and cushion forms, but is specially characterized by the long divergent branches which tend to be circinately curved at the tip so that the plant has an open, incipiently drooping facies.

### 2. *Degree of Hairiness.*

This character and one other (berry colour) are the most important and conspicuous of all, and upon them is based most of the taxonomy of the genus.

The epidermal appendages in *Empetrum* are of two perfectly distinct kinds. The lips of the slit leading into the leaf-cavity are furnished with numerous long, unicellular trichomes or hairs, which meet and interlace across the opening of the slit. The cavity of the leaf contains a much smaller number of multicellular capitate glandular hairs. These two distinct kinds of appendages are found in all *Empetrum* plants in varying degrees of development and proportion. For the sake of brevity the long unicellular structures are, in the following paragraphs, referred to as hairs and the capitate glandular structures as glands.

All specimens of *Empetrum* show the two close rows of hairs on the lips of the leaf-slit and also some glands inside the cavity. On this account and because differences in these features are not apparent externally they are not further mentioned.

It is convenient to take first those specimens which, apart from the underside of the leaf, show least hairiness. In these plants hairs are developed only in the region of the vegetative buds. Here they function, in part at least, as protective structures for the developing leaves. They are very soon shed, and do not serve to give any distinctive appearance to the plant as a whole. Glands, on the other hand, are found fairly evenly and plentifully over the epidermal surfaces of the stems, in much fewer numbers on the true leaf-edges and more rarely still actually upon the leaf-blades. In the most nearly glabrous forms they are minute and confined to those parts of the stem near the leaf-bases.

In those plants in which hairiness is most marked the hairs are present in very great numbers and are abundant all over the stem, on the true edges of all the leaves, and on the surface of the younger leaves. The buds and tips of the vegetative branches are almost hidden by them, and the whole plant is conspicuously white-hairy, with the exception of the actual blades of the mature leaves.

Such then are the two extreme conditions, seen in the genus. The remaining specimens form, in hairiness, a complete series of intergrades between the two. From one end to the other of this series the glands first become more plentiful and more conspicuous, and then the proportion of hairs gradually increases until they become almost entirely predominant.

As regards these extreme conditions there is very marked geographic segregation. The very hairy forms may be said to be confined almost entirely to the Southern Hemisphere, while the more glabrous condition is generally confined to the north. It is therefore of interest to trace the occurrence of more hairy forms in the north and glabrous forms in the south.

The most hairy specimens of the north are found in the extreme east of N. America. In these the stems are covered with white hairs, but the leaves have only a small number of glands. These plants also have a procumbent habit and often very small leaves. Other specimens from neighbouring localities have white hairy branches, but the hairs are much fewer in number and, as before, are absent from the leaves. This condition of hairiness can be closely matched by individual specimens from Japan and Siberia. In all of them the expanding leaves have hairs, but these are soon shed and the mature leaves have none. The remaining N. American plants belong on the whole to the more glabrous (glandular) type, but here and there individuals occur in which the hairiness is much increased and there is a thin tomentum on the stem, but these plants are rare and not geographically segregated.

Greenland specimens in general tend to show slightly increased hairiness. Glands are abundant and well developed on the stems and less so on the leaves, and hairs occur in the buds and may persist for a short time after leaf-expansion. The most glabrous specimen of all was amongst those examined from the Faeroes. Here the hairs were absent and the glands very sparse, particularly on the stems. In the case of the hairs it must be remembered that they naturally appear to be more conspicuous in plants collected during the expansion of the vegetative buds, while specimens collected in winter would be unlikely to show them at all. Due allowance must be made for this in comparing different conditions. Arctic specimens in general illustrate a condition of strong glandulation and transitory apical hairiness. In some cases a single gland at the extreme tip of the leaf-apex may be particularly strongly developed.

Nearly all the British specimens belong to the general glabrous type (the term is used in a comparative sense), but some Scottish specimens have numerous hairs in the bud regions, and these may persist for a time. Practically the same remarks apply to the European continental plants. In general, transitory hairs are present and the stems are rather strongly glandular, with a certain proportion of hairs. On the other hand, the stems may bear only a few glands. Such a state is seen from the Alps as well as from other localities, but is not particularly characteristic of plants from such places.

Asiatic plants also generally illustrate the more glabrous condition, but increased hairiness tends to be common in plants from the Far East (Kamchatka and Japan), and plants are generally found with a thin but definite brown tomentum on the stems.

Turning now to the Southern Hemisphere, the condition of affairs is reversed. The great majority of specimens examined belong to the hairy type, while glabrous ones are comparatively rare. The most hairy forms of all are those of the Falkland Islands. In these a copious tomentum of long white hairs covers the stems, the whole of the young leaves are covered with them, and they persist on the edges of even the oldest leaves. These plants, however, belong to the cushion type, and so do not retain their leaves as long as the majority of individuals. The obvious result of this degree of hairiness in the Falklands plants is that they are conspicuously white-lanate.

On the continent of South America a wider range of variation is found. Here the plants are mostly hairy, but generally less so than they are in the Falklands, but found with these are all stages to a condition as glabrous as the majority of northern specimens. These forms, in which hairs are absent and glands plentiful, are chiefly to be found in the Andes and on the western coast of the continent. The specimen from Juan Fernandez, on the other hand, approaches the very hairy condition.

The specimens from Fuegia and from the Tristan da Cunha group belong mostly to what may be termed the intermediate hairy condition, in which the stems are thinly lanate and with many hairs, but the leaves, when mature, have glands only.

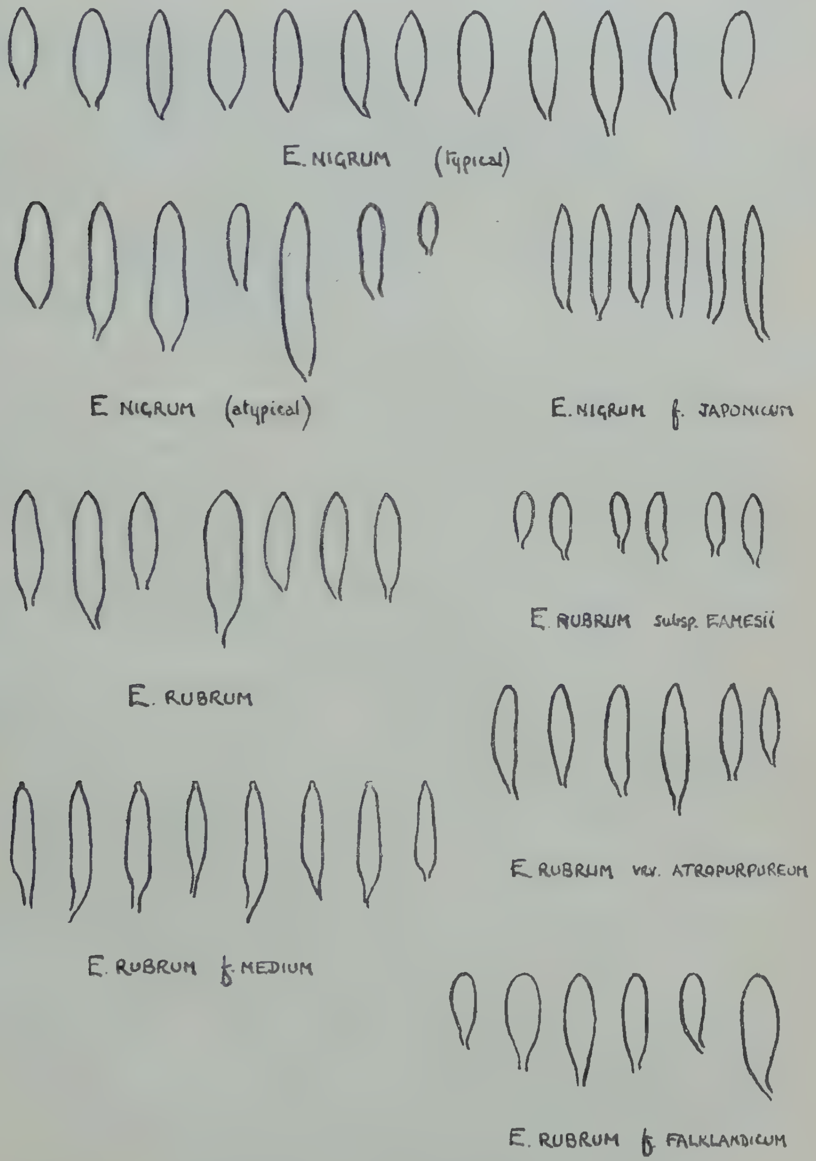
In the foregoing very short and incomplete account it has been impossible to mention any but the more important features of variation in hairiness. The chief point is that, taking the genus as a whole, there is every intermediate stage between the most glabrous and the most hairy conditions, but coupled with this is a considerable amount of geographical segregation.

### 3. *Shape and Size of Leaf.* (See fig. 4.)

It is convenient to consider under the single heading of shape and size of leaf several distinct variational series which, in combination, cause those differences of foliage not referable to the number and position of the individual leaves.

Since shape is a much more important descriptive feature than size, it is here dealt with first. To convey the shape of a leaf completely, two items must be described—namely the surface and the profile. The general form of leaf-surface in *Empetrum,* the form which is commonest and from which the others seem to diverge, is a very narrow acute ellipse in which the long axis is about four times the short axis. All *Empetrum* leaves are shortly petiolate, and the transition from blade to petiole is narrowed. Such generalised proportions in leaf-dimension are found in the majority of specimens, whatever their locality. From it four variational tendencies are discernible. These are towards increased narrowness, increased breadth, a broadening at the tip and a broadening at the base. The first of these is fairly common, and is particularly well-marked in specimens from Japan, Eastern Asia, and parts of western North America. Its furthest expression is reached in Japan, where the length of the leaf may be as much as six times its breadth. Associated with this is a tendency towards straight and parallel sides, rather than to the general narrowing of an elliptical outline. It is also present much more rarely in the Southern Hemisphere, especially in Tristan da Cunha. Here it is usually associated with increased basal breadth. These leaves from Tristan are particularly interesting because they illustrate an apparently unique trend in leaf-shape. This is towards the production of a definite apiculus at the tip, and such a feature is sometimes strongly marked.

Fig. 4.



Leaf-variation in the genus Empetrum. × 2·5.

Increased breadth of leaf also occurs in small proportion over most of the plant-range, but this condition is more emphasised in specimens from the

Alps and from the Southern Hemisphere, especially from the Falklands and South America. Some Scottish plants show it in lesser degree. In its fullest expression the leaf has a regularly elliptic outline and a length up to two and a half times its breadth. The most marked condition is seen in certain Scandinavian plants.

Increase of breadth towards the tip is associated with increasing roundness of the tip. This is not a common trend, but is widely distributed, though it is best and most often seen in southern specimens. It is most marked in the Falklands, where the leaves may be very narrowly but quite obviously spathulate. Similar leaves occur on some Scottish specimens. Such leaves are usually ascending, and are not often found reflexed.

The reverse of the above, namely increase of breadth near the base of the blade, also has a wide range, but is chiefly found in Europe, North America, and the Arctic. It is also seen associated with the apiculate leaves mentioned above from Tristan. In such leaves the transition into the petiole is more rounded and the petiole itself is generally short.

Rarely individual leaves are found in which the long axis is not quite straight, so that from above the outline of the blade is slightly sickle-shaped. This is never sufficiently prominent to be a feature of the total foliage of a plant, and appears to be an anomalous condition. It is usually found in narrow parallel-sided leaves.

Variation in the profile of the leaf is much less conspicuous than variation in the outline of the blade. Typically the profile has straight and parallel edges, or, in other words, the leaf-blade is flat and of a similar thickness throughout. In many cases, however, without geographical significance, the profile is curved so that the long axis of the blade is slightly concave. The reverse curvature is also seen so that the blade axis is convex. This is best seen in specimens from Tristan. A more marked difference is seen in leaves where the profile, while still straight-sided, is thickened towards the tip. This results in a somewhat club-shaped leaf, and occurs chiefly in leaves with a rounded apical outline. This type is particularly, but by no means exclusively, found in specimens from the south and more especially from the Falklands. Here again the edges of the profile may be curved so that the blade is concave. This curved and apically thickened profile is often associated with the spathulate outline, and when all these characters are present a very noticeable type of leaf is seen which occurs principally in the cushion plants of the Falklands. These differences in leaf profile are quite possibly more conspicuous in dried material than in fresh, but they are presumably the outward sign of a difference in internal structure.

A good deal of difference is apparent in absolute leaf-size, but all observed cases fall within certain distinct limits. No leaf has been seen by the writer which is more than 9 mm. long. This size itself is unique, and occurred in a specimen from Labrador in which the total number of leaves was very small.

In the opposite direction no adult leaves have been seen less than 2 mm. in length. This extreme figure was unique too, and occurred in a specimen from Fuegia. Omitting these exceptional records, it may be said that the length of the leaf varies from 3–7 mm., and the vast majority are from 4–6 mm. As regards breadth, this is really only significant in conjunction with length, and the various proportions of the two dimensions have been mentioned already. In absolute range, however, no leaf seen was less than 1 mm. or more than 2 mm. in breadth.

Although size is a character which varies from one individual leaf to another in the same plant, in some cases there is a definite tendency. This is found usually in certain individuals which occur only on the islands and part of the seaboard of eastern North America. In these the leaf size is constant but remarkably small.

### 4. *Arrangement of Leaves.*

The character of leaf-arrangement shows a very wide range of variation. It is difficult to say what is the basal or normal design, and it seems that a variable arrangement is quite a usual feature. This is borne out by Hagerup's (**17**) study of the Danish plants and their leaf-arrangement, and his remarks may be shortly repeated here. He finds that in the primary seedling shoot the leaves are always opposite, but as the plant develops so the leaf-arrangement becomes more complicated. The second stage is a spiral with a 2/5 divergence, the third is a whorl of three, the fourth is a 2/7 spiral, and so on even up to spirals of 2/11 and 2/12. A shoot may show two or three of these on different parts, and the transition is usually without any intermediate stages. If two of these arrangements are spirals they are antidromous.

Although Hagerup treats the whorled arrangement as a numerical form of the spiral, it is remarkable that arrangements of these particular values are always true whorls and not spirals. For example, the arrangement 2/6 is never a true regular spiral, but is always in the form of one 6-leaved or two 3-leaved whorls. This, of course, is because the vertical intervals between successive leaves are not constant, but vary in a remarkable degree. It is to this that the conspicuous differences in leaf-arrangement are due. Differences in regular spirals with only different numerical values is comparatively slight. In procumbent shoots a difference is more apparent because the leaves tend to twist into a two-ranked dorsiventral system.

This unequal leaf-spacing leads to a number of marked features. The most common is the production of distinctly whorled leaves on long robust shoots. In such cases the spiral numerical figure is a high one and the resulting whorls are many-leaved. On the other hand, where the basal spiral number is low and the vertical leaf-distances are very small but constant, an arrangement results which is best described as "pseudoveronicoid," and may be even very closely decussate. This type is particularly characteristic of the bushy and cushion forms, especially the latter, and is presumably correlated with the short axes and profuse and close branching of these plants.

Still another apparent arrangement results from the fact that the vertical distances between leaves may actually vary from leaf to leaf. This tends to result in the loss of any regularity in arrangement, and such a condition may be termed scattered. In some cases more or less distinct whorls are joined by one or two scattered leaves on the comparatively long internodes, while in others the true spiral and the whorl are both lost. These types are found chiefly among the luxuriant specimens of the lower levels of the northern zone.

The absolute number of leaves also varies very markedly, and often associated with long-growth increments is a marked diminution of leaf number. On the other hand, it is in the bushy and cushion plants that the most leaves and closest arrangements are found.

### 5. *Angle of Leaf-insertion.*

A variation closely correlated with that of leaf-arrangement is seen in the angle of leaf-subtention. Broadly, the leaf may assume one of three positions with regard to the axis which bears it : it may be ascending or at an acute angle, it may be spreading or almost at right angles, or it may be reflexed or at an obtuse angle. The simplest cases are those in which all, or nearly all, the leaves are of one of these types, but this is rather rare. It is best seen in the bushy form and in some of the cushion plants where the foliage is predominantly ascending. Similarly in some Arctic and northern specimens nearly all the leaves tend to be reflexed.

It is much more common to find that the leaves at different levels on the plant assume different positions. The younger leaves when they first emerge from the bud are almost vertical, then gradually as the growing point of the shoot advances they become more spreading, and finally some time before they fall they become reflexed. This type is the most general and the most widely distributed, but very often the story is not completed or the leaves remain in one condition an unduly long time. Closely connected with this is the very varying lengths of time that the leaves persist. This time may extend to several years. In some cases the leaves are shed when still green, but in others they may persist long after they are brown and withered.

It often happens among the procumbent forms that nearly all the leaves, even quite close to the growing point, are reflexed. This is well seen in some of the eastern North American and eastern Asiatic plants, but the reflexion is not very marked and usually scarcely more than horizontal. This is not the same feature as is mentioned above in certain Arctic specimens.

### 6. *Sex of Flowers.*

Although unisexual flowers are normal in the genera of the Empetraceæ, in *Empetrum,* at any rate, functionally bisexual flowers very frequently occur. It is usual to find rudimentary staminodes, which are developed to a greater or lesser degree but which do not become functional, and so the truly hermaphrodite condition seems to be only the ultimate expression of this variable condition. It may be said that the hermaphrodite condition may be found almost anywhere in the generic range, but is especially common and characteristic in high latitudes and altitudes. It is usual in plants from Arctic regions, and also occurs in plants from alpine localities, such as the Canadian Rockies and the Alps, and also frequently among the plants of the Southern Hemisphere. On the whole, unisexual flowers are much more common, and in many regions, such as Great Britain and Japan, any other condition is almost unknown. In the former the only evidence to the contrary is a drawing, by Salisbury, of an hermaphrodite plant which is thought to have come from Scotland. In the Southern Hemisphere there does not seem to be the same correlation between hermaphroditism and latitude and altitude as there is in the north.

The vast majority of *Empetrum* plants are either completely hermaphrodite or strictly diœcious, but other conditions also occur rarely. A polygamous state, in which hermaphrodite and unisexual flowers occur on the same plant, has been described by Skottsberg from Fuegia and by Fernald and Wiegand from eastern North America. Similarly a monœcious condition has been reported from time to time.

As to the proportion between the sexes in unisexual plants, female individuals seem to preponderate, but this may be due to the fact that the berries make them conspicuous and more often noted or collected.

One other feature seen occasionally is a change in sex of the same plant from year to year. A case is reported in which a plant produced male flowers in 1908, but in 1910 half the flowers were male and half female. This seems to indicate that while the plant is potentially hermaphrodite it is usually unisexual by abortion.

### 7. *Berry Colour.*

Difference in berry colour is the character most obvious in superficial examination, and most often used as a basis for the segregation of individuals.

The berries of *Empetrum* may be black, purple, red, or white. The red berries may be either dull full red or a paler translucent red. The interest of these different berry colours is that there is considerable geographical correlation associated with them. First and most noteworthy, *all the plants* of the Southern Hemisphere have red berries. No specimens appear to be extant in which any other colour is indicated. The only doubt upon this generalization is the statement of the traveller, R. O. Cunningham (7), who, in speaking of Port Gallant, says, "The *Empetrum* . . . bearing red and purplish-black berries in nearly equal abundance." In absence of confirmatory specimens the statement can hardly be accepted without reserve.

In the Northern Hemisphere the matter is rather more complex. The very great majority of plants have black berries, but the following exceptions occur. A group of plants found only in extreme eastern Canada and the U.S.A. is characterized by having translucent red berries. Another group from the same region has purple berries. The normal berry in the north passes from green to black and not through a red state, so that these colours cannot well be temporary states. Ordinary opaque red berries are found in the north very rarely and sporadically and chiefly in the Arctic regions. Simmons states that many of the *Empetrum* plants in Ellesmereland have red berries.

The occurrence of white berries is a somewhat obscure phenomenon. They have been reported several times from the Baltic region, but the records are short and it is not quite clear what is meant by "white berries." It is possibly a pathological condition associated with the presence of the fungal genus *Sclerotinia.*

To summarize: *Empetrum* in the south always has red berries; the great majority of the northern plants have black berries, but red or purple ones occur rarely and white have been recorded.

Although only seven characters have been described above, it must not be supposed that they are the only variable ones. If a sufficiently extensive series of specimens is examined, it will be found that every possible character varies to a greater or lesser extent. Most of these are characters which are comparatively valueless as taxonomic characters, and from this point of view are of secondary importance. It is not possible or desirable to mention all such characters, but the following will serve as examples:—

1. The colour of the floral parts varies from greenish to some shade of red. The colour is often darkest in the anthers, and these are sometimes almost black. Such a condition is seen among some European plants. The flowers of the plants in the Falklands are often more highly coloured than is usual. The greenish flower is apparently very rare, and the writer has seen only a single specimen from Sweden. This plant has been called forma *leucandra.*

2. Another floral feature is the length of the filaments. In such a case a good deal presumably depends upon the stage of growth at which the flower is observed, but it is clear that the length of the mature filament does vary considerably.

3. The number of seeds in the berry may vary between one and nine, and the branching of the stigmas may also vary. Not only the number, but also the size of the seeds fluctuates, and this in turn possibly influences the size of the whole berry. Some are quite twice the size of others, but all those of a single plant are usually about the same size.

4. The leaves are usually shed before they begin to wither, so that the plant bears only green leaves. Sometimes, however, the dead and brown leaves persist for a considerable time and the plant has quite a distinct facies. This condition seems to be commonest in Arctic regions.

5. There is also a good deal of difference in the time of flowering. In the southern part of the generic range this begins in late March or early April, but farther north or at higher elevations it becomes progressively later till, at least in parts of the Arctic, it commences so late that the remaining summer season is not long enough to allow the ripening of fruit. This feature is not truly a variable character; it is merely an expression of geographical and topographical position.

The most important fact emerging from the foregoing account is that variation is not always of the same type. It is, in fact, possible to recognize three types, *i.e.* continuous, compound continuous, and discontinuous.

### 1. *Continuous variation or variations in a single character and direction, and with all intermediate conditions from one extreme to the other.*

This is the usual simple expression of the phenomenon of continuous variation, and is seen at its best in *Empetrum* in the character of hairiness. There is a considerable degree of difference between the two extreme forms, but there is also practically every possible intermediate condition between the two. The actual basis of this variation is very obscure. It may of course be suggested, according to the usually provided explanation, that increased hairiness is of value to the plant in enabling it to live in certain localities where cold is intense or winds are high so that there is danger of excessive transpiration. However, when tested this explanation does not meet the case. Arctic plants are not markedly more hairy than are Andine and Alpine plants. Again, the climatic conditions between the Faeroes and the Falklands are said to be very close, especially as regards strong winds. Yet the specimens from the first are among the most glabrous, while those from the second are the hairiest of all. As has been stated, part of the hairy covering consists always of multicellular glandular hairs. It is difficult and against reason to imagine these are produced without any reference to the substance which they are designed to secrete, and so it must be assumed that the number of glands is some measure of the production of this secretion by the plant. If so, then the phenomenon of hairiness, in part at least, is closely correlated with the biochemistry of the plant, as this in turn is most probably dependent upon the external supplies of raw materials. In the case of the hairs it is possible that the actual potentiality for their production in a definite quantity may be a simple genetical factor.

### 2. *Compound continuous variation.*

This is a condition of continuous variation, but the direction of the trends are such that it is not possible to place all the intermediate conditions in a single straight series. Actually the whole variation is made up of several variational themes on the same member. A very good example is afforded in *Empetrum* by the character of leaf-shape. Here there is a general central, common shape found all over the plant's range. From it continuous variation occurs in several directions. For example, there is variation in the length–breadth index; then there is a variational series from the central form to leaves which are abnormally broad at the base or, in another series, at the tip, and there is a series with a tendency towards the production of an apiculate leaf-tip. Other trends are towards tip-thickening and leaf-curvatures. It is true that each of these elements could be separated and treated as a single variational series, but such a separation would be very artificial. Differences of leaf-shape in *Empetrum* are caused by the interaction of them all. The whole phenomenon is best visualised as a single central type or condition occupying the centre of a circle and the various extreme forms lying at the ends of a similar number of radii diverging from the centre. In certain cases two radii may be continuous on either side of the centre, indicating a continuous series in which the common general type is in the middle position rather than at one extremity. These variational trends appear to be inherited and emphasised from generation to generation, and there is also a considerable degree of geographical correlation. The trend towards apiculate leaf-tips is found only in plants from the Tristan group, and the Falkland leaf-type is also rather peculiar. It is probable that this condition of affairs, when numerous trends are present, but the great majority of individuals conform to a generally inconspicuous mean form, indicates that within the unit called the genus *Empetrum*, or even within the family, variation in leaf-form is a comparatively recent innovation which has not yet settled down to any particularly emphasised trend in a given direction.

### 3. *Discontinuous variation.*

A particularly good example of discontinuous variation is seen in the berry colour. Five quite distinct conditions are found, and, as far as is known, there are no intermediates between them. The commonest condition is black, rather less common is red, still rarer are translucent red, purple, and white. It seems probable that these differences arose as mutations, and that the occurrence of the colours is easily explained on a simple genetical basis, such, for example, as the presence or absence of melanic or colour-intensifying factors. It does not seem likely that hybridism has played much part except conceivably in the case of the purple berries. Here it is significant that this particular colour is found close to and in part actually overlapping the only portion of the generic range where both red-berried and black-berried plants are found. The difference between the two types of red berry is quite distinct even in a dry state, and possibly the white berries show a somewhat analogous loss of colour in certain black-berried plants.

The second interesting feature revealed in the description of the variable characters is the occurrence of correlated variation. This is seen when one definite condition in one character is always accompanied by a definite condition in another character, and the subject is so important from the taxonomic point of view that its occurrence in *Empetrum* is worthy of further discussion. The most striking example of this is in the close correlation between the degree of hairiness and the colour of the berries. All red-berried plants are invariably much more hairy than black-berried ones, and include those forms in which the hairiness is greatest. Extreme hairiness is never found in black-berried plants. Similarly glabrous red-berried forms are almost lacking, although such a condition is seen among Andine specimens. Associated with this correlation is a third character, that of growth-form. Whether this feature is due to the influence of external factors or not, it is remarkable that, whereas the procumbent form may be associated with either red or black berries, the bushy form is mostly found in plants with black berries, and therefore less hairiness, while the cushion form is always found with red berries and increased hairiness. Since berry-colour has a geographical significance, so also has the variable characteristic of plant-form, and, as a general rule, cushion plants are found in the south and bushy plants in the north. The procumbent form, on the other hand, is found in both regions, and also shows no correlation in hairiness and berry-colour. Again, apically broadened and thickened leaves are almost always associated with cushion form, marked hairiness, and red berries. Such leaves, however, do occur rarely among black-berried plants of the north, but when this is so it will be found that the plants are more hairy than usual. Similarly, basally broadened flat leaves may be found with both red or black berries, but not in the cushion plants or where hairiness is very marked. They are usually associated with a semi-erect open habit, but do not occur in cushion plants. Apiculate leaves and a tendency to circinate branches also are similarly associated with a semi-erect open habit, and are themselves only found in conjunction. Black-purple berries, whatever their significance, are always found in plants with procumbent habit, medium hairiness, and large leaves. Translucent-red berries are in their turn always found associated with very small elliptic leaves and considerable hairiness. Many other similar but less-marked examples might be mentioned, but enough has been said to show how common is correlated variation and to what extent the characteristic facies of the plants are due to it.

Taking into consideration the amount of intra-generic variation described above, it might, with some reason, be supposed that any attempt to classify the contents of the genus would be either very difficult or altogether impossible. The genus might well be pictured as composed of a large number of individuals no two of which were exactly alike, but all showing a very similar degree of relationship among themselves. The genus would, in fact, be monotypic, containing only one variable taxonomic unit. The actual facts are entirely different. Almost every specimen of *Empetrum* can be placed without any doubt into one and only one of a small number of categories different in appearance and capable of concise but distinguishable descriptions. This is almost entirely due to the combined effect of the phenomena already described, namely correlated variation and geographical segregation.

A careful examination of a sufficiently extensive series of specimens shows that in the genus *Empetrum* it is most convenient and most in accordance with the facts of variation and distribution to recognize ten categories or taxonomic units. To recognize less will be to ignore obvious and important phenomena, and will necessitate grouping together individuals which show considerable difference. To recognize more than ten will necessitate the use of differential criteria of such sort and magnitude as would be quite impracticable, and which would lead to the recognition of taxonomic groups which would be almost indefinable and without any geographical significance.

These ten kinds of individual which should, in the writer's opinion, be recognized are described below. Each kind is denoted, for the time being, by a letter of the alphabet, the question of nomenclature being deferred until later. Two points must be borne in mind in reading the descriptions—firstly that the characters are mostly described in comparative and therefore inexact terms, such as "long" and "short," and secondly that the description is that of the usual condition of the plant in question. As stated above, there are individuals which are more or less intermediate between two of the descriptions.

A. Plant usually procumbent, but sometimes rather bushy. Never cushion-like. Stems with glands only. Leaves glabrous, rather large, not closely set, mostly ascending or spreading, narrow elliptic, not very acute. Petioles short. Flowers usually unisexual, but in higher latitudes and altitudes often hermaphrodite. Berries black, rather large.

Throughout the whole northern range of the genus with the possible exception of part of Japan.

B. Plant usually procumbent, more rarely rather bushy. Stems glandular or slightly hairy. Leaves glabrous, many and close-set, nearly all reflexed-imbricate, very narrow, linear acute. Flowers unisexual. Berries black.

Almost confined to Japan and Saghalien, but also occurs rarely in other parts of eastern Asia and in Europe.

C. Plant procumbent. Stems densely but shortly white-hairy. Leaves glabrous, small, closely set, mostly ascending, narrow elliptic, rounded. Flowers unisexual. Berries rather small, pale translucent red. Confined to granitic and siliceous parts of Labrador, Newfoundland, and the coasts of Saguenay, County Quebec, all within the range of A.

Two specimens, one from Juan Fernandez and one from Fuegia, exactly correspond vegetatively, but there is doubt as to the berry colour.

D. Plant procumbent. Stems densely white- or brown-hairy, at least when young. Leaves glabrous, rather large, not closely set, mostly ascending, narrow elliptic, rounded. Flowers unisexual. Plants sometimes polygamous (10). Berries few, large, dark purple.

Confined to granitic and siliceous parts of Magdalen Islands, Prince Edward Island, and mountains of Maine, New Hampshire, and possibly Vermont, all within the range of A.

E. Plant procumbent. Stems glandular. Leaves glabrous, rather large, mostly ascending, not very closely set, narrow elliptic. Flowers unisexual or hermaphrodite. Berries red.

A little-known plant, occurring here and there in the American Arctic Archipelago and possibly also in Greenland and the Old World Arctic. All within the range of A.

F. Plant procumbent. Stems glandular. Leaves glabrous, rather large, not closely set, narrow elliptic. Flowers unisexual. Berries white.

Another very little known plant, recorded from Western Gothland, Finland, and other parts of the east Baltic coast, within the range of A.

G. Plant generally bushy, more rarely procumbent. Stems more or less densely hairy. Leaves glabrous or slightly hairy when young, not very closely set, mostly ascending, rather large, narrow elliptic, but often broader at one end than at the other. Petioles sometimes rather long. Flowers unisexual or sometimes hermaphrodite. Berries red.

All over the Southern Hemisphere range of the genus.

H. Plant bushy rather than procumbent. Stems glandular only. Leaves glabrous, rather large, not very closely set, mostly ascending, narrow elliptic or broadest at the base. Petioles sometimes rather long. Flowers unisexual. Berries red.

Range somewhat uncertain, but mostly confined to the western side of the Chilean Andes. Occurs also in Fuegia and S.W. Patagonia.

K. Plant of open semi-procumbent habit. Stems more or less densely brownish-hairy. Leaves glabrous, rather large, not closely set, mostly ascending, but with a distinct outward curvature and with a marked apiculus, narrow, rather broader at the base. Petioles long. Flowers numerous, dense, usually hermaphrodite. Berries red.

Confined to the island group of Tristan da Cunha and Gough Island.

L. Plants of cushion habit, sometimes very large. Stems densely white or brownish-hairy. Leaves, all but the oldest, with white-hairy edges, numerous, not very large, closely set, mostly ascending imbricate, rounded thickest and broadest towards the tip, narrow elliptic or spathulate. Petioles short. Flowers unisexual. Berries red.

Almost confined to the Falkland Islands, but also found rarely on the South American continent.

## TAXONOMY.

Before discussing the relationships of the various plants described above, it will be interesting to summarize the treatment they have already received at the hands of taxonomists.

The modern taxonomy of the genus *Empetrum* begins with the publication of Linnæus's 'Species Plantarum' in 1753 (**25**). In this work a single species, *E. nigrum*, is described. The description is very short, but the type-specimen in the Linnæan Herbarium is typical of description A. In 1792 Gilibert (**15**) described a species, which he called *E. procumbens*, from near Grodno, on the Niemen. There is no type-specimen, but from the description and also from the fact that the author cites *E. nigrum* apparently as a synonym, there is no doubt that this plant also belongs to A. In 1805 Vahl (**26**) first described, as *E. rubrum*, a plant from the Southern Hemisphere. The type-locality was Straits of Magellan, and the type-specimen answers to the description G (p. 511). Some years later (1818) Carmichael (**6**) described under the name *E. medium* a plant from Tristan da Cunha. The type is in Herb. Brit. Mus. and the plant is that described under K above. In 1830 W. J. Hooker (**20**) referred under the name *E. scoticum* to a bushy form of *Empetrum* grown in gardens. The artist R. A. Salisbury made drawings of this plant and these, together with a tiny specimen named in his own hand, are in Herb. Brit. Mus. The plant belongs to the blunt-leaved, rather hairy hermaphrodite type. As there is no evidence of its occurrence anywhere in a wild state, it has not been further considered in this paper. In 1836 two new species were described by Rafinesque (**31**). One of these, *E. crassifolium*, has no type, but the very inadequate description indicates that it falls under A. It is said to come from Siberia. The other species, *E. purpureum*, has led to a great deal of taxonomic confusion. The facts cannot be discussed here, but they have been summarized admirably by Fernald and Wiegand (**12**). Their researches show without much doubt that the plant meant is that described under E.

The taxonomy of the genus was first summarized by A. de Candolle (**5**) in 1869. This author proposed one species, *E. nigrum*, and three varieties. The first, *b. purpureum*, was formed by reducing Rafinesque's *E. purpureum* to varietal rank. The second, *c. andinum*, was based on a plant distributed under the name *E. rubrum* Vahl, and with which was also associated the name *E. andinum* Phil. This latter is a *nomen nudum*. From the descriptions of the varieties given by de Candolle, his var. *andinum* is the plant described above under H, but the actual specimen quoted is not a very good example of this plant-form. The third variety, *d. rubrum*, was made by reducing *E. rubrum* Vahl to varietal rank.

No other species were described until 1913, when three new ones appeared. *E. Maclovianum* Gandoger was published with a most inadequate description, but the type-specimen, collected by Skottsberg (**37**) in the Falklands, belongs to description L (**35**). The other two species were described by Fernald and Wiegand (**12**) from eastern North America. *E. atropurpureum* is the plant described in D; *E. Eamesii* is the plant described in C.

Varietal or lesser names are mentioned in the synonymy given on page 519.

It now becomes necessary to construct some plan of the genus which will express as adequately as possible the various phenomena described in the preceding pages.

The first question to be decided is whether the genus is to be regarded as monotypic. It may be said at once that the point upon which the decision has hung has always been that of the relation between the black-berried northern glabrous plant and the red-berried hairy southern plant. By some they have been considered specifically distinct, by others the latter has been considered but a variety of the former. Hooker, in 1846, expressed his opinion at some length. At that time the problem was rather simpler because, so far as was known, only black-berried glabrous plants were to be found in the north, and only red-berried hairy plants were known from the south. It seemed that there was not only complete morphological difference, but also complete geographical distinction. Hooker was of opinion that these two facts, taken together, were sufficient to warrant the view that the plants of the north and south were distinct species. Since that time the question has become much more complicated. This is particularly due to the discovery of hairy red- or purple-berried plants in the north, and the discovery that a red-berried glabrous form is to be found in either region. It will therefore appear that both of Hooker's criteria of specific distinction have failed; but this is not quite a true view of the case. The red-berried glabrous plant of the north occurs sporadically among ordinary black-berried plants, from which it is distinguishable only in the berry colour. It is clearly a colour-form of the black-berried plant. The red-berried glabrous plant of the south, on the other hand, is found among the ordinary red-berried hairy southern plants, and differs from them only in being very much more glabrous, even completely so. It is as clearly only a glabrous state or form of the hairy southern plant. This being so, it is obvious that the apparent similarity between these glabrous red-berried plants has no significance from the point of view of taxonomy. This raises a very interesting theoretical point which will be discussed more fully later.

The second difficulty in maintaining Hooker's view is the occurrence of red- or purple-berried hairy plants in the north. As has been explained above, hairiness is a very variable character, and some plants are very much more hairy than others. Nevertheless the only two plants of the north showing hairiness at all comparable in degree with the condition normal in the southern plants are the plants described above as C and D. Neither of these has black berries, nor are black berries ever found associated with a similar degree of hairiness. In D the berries are purple-black and in C they are pale translucent red. Thus Hooker's morphological criterion still exists, and it is possible to divide the individuals of the genus into those with hairy stems and red or purple berries and those with glabrous stems and black berries. Both these plants may produce red-berried glabrous forms, but these are not taxonomically identical. His geographical criterion requires modification. The black-berried glabrous plant is still found only in the Northern Hemisphere, but the red-berried hairy plant is now known from the north as well as from the south. Curiously enough, both northern forms of it are narrowly confined to different regions in the same part of North America. Their ranges here are almost distinct, but both are found in Labrador. When the presence of these plants was first detected, it was supposed that they were both peculiar to the north. It is, however, very uncertain whether this is true. Under these circumstances the geographical criterion of Hooker has only in part and not entirely disappeared. One of his two species is still confined to one hemisphere, while the second is now known to have outliers or related forms in the north. Is it still justifiable to admit the two species? It is significant that in eastern North America, where representatives of both potential species are found over the same region, there are no signs of hybridization or of intergrades. The only possible example of such is the occurrence among Newfoundland specimens of glabrous black-berried plants with small leaves rather like those of plant C. Careful examination shows that this similarity is more superficial than real, and it is very unlikely that there is any connection between the two plants. The black-berried northern plants show a slight tendency to small leaves in other parts of its range. Taking all these facts into consideration and taking general convenience also into account, it is both desirable and justifiable, in the writer's opinion, to maintain the specific difference between the two plants under discussion and to recognize two species, *Empetrum nigrum* Linn. and *Empetrum rubrum* Vahl.

After careful examination of the other forms of the genus, it will almost certainly be agreed that if these two species are kept up they are the only forms within the genus to which specific value can be attached. All the rest must fall under them as subsidiary units. It is therefore necessary to decide just what category shall be applied to each. It will be convenient to deal with the different plants in the order in which they are described above.

Plant B has black berries and therefore belongs to *E. nigrum*. From this plant it differs very much in superficial appearance owing to the greater number of leaves, their extreme narrowness, and the reflexed position which they normally assume. This distinction is not absolutely sharply marked, and although in its extreme condition it is at once recognizable, there are intergrades between it and *E. nigrum* proper. Plant B also has no distinct range of its own. It is proportionately very abundant in eastern Asia, and in Japan is perhaps completely predominant; but farther west it becomes more and more rare among ordinary *E. nigrum*. In other parts of the north it is seen sporadically in modified condition. Under these circumstances B must be treated as a form of *E. nigrum*. It has not been given taxonomic rank before, and owing to its abundance in Japan it is convenient to call it *E. nigrum* forma *japonicum* *.

Plant E is the red-berried glabrous plant already mentioned above. It occurs sporadically among *E. nigrum* in Arctic regions, especially in Ellesmereland, and differs from that plant only in the berry colour. It must certainly be considered as a second form of *E. nigrum*. The question of the name is a little difficult. It is presumably to this plant that the name *purpureum* was originally given by Rafinesque. The plant is here called *E. nigrum* forma *purpureum*.

Plant F is an even less known plant. It is extremely similar to *E. nigrum*, and, in fact, differs only in having white berries instead of black. It is not quite clear what is meant by white berries, but it is significant to note that a similar condition is seen in certain other berried plants, especially Ericaceæ and Vacciniaceæ, and has there been associated with the attacks of fungi belonging to the genus *Sclerotinia*. Whatever the actual cause of the condition, plant F cannot be considered other than as a form of *E. nigrum*. It has already been described as such under the name forma *leucocarpum*. It has no real distribution, but the few records are all from the Baltic region.

It may be mentioned in passing that the rather similar formal name *leucandrum* has applied to certain male plants in which the flowers and particularly the anthers are very pale in colour. Such a character is extremely variable, and anthers may range from pale green to very deep purple.

The next two plants to be considered are C and D. These are the red- or purple-berried plants with hairy stems, and so, although found in the north, must be placed under the southern species *E. rubrum* rather than under *E. nigrum*. Plant D differs from *E. rubrum* only in the colour of the berries, and if it was found or was known to grow among *E. rubrum* itself, it could not be treated as other than a colour-form of that species. Actually it occurs as far as is known only from North America, whence no typical *E. rubrum* is known. The only reason for doubting the truth of this is Cunningham's statement that he had seen purple-berried plants in Magellan. It has been suggested to the writer by Prof. Skottsberg that the "purple" fruit was actually over-ripe and withering red fruit. At all events, there are no specimens of southern purple-berried plants extant, and there is no real reason for supposing their existence. It therefore seems that associated with the difference of berry colour is complete geographical segregation from *E. rubrum*. This being so, it seems reasonable and best to treat it as a variety of *E. rubrum*. It has already been described as a species, *E. atropurpureum*, and it may therefore be called *E. rubrum* var. *atropurpureum*. This view is based upon what is known of the plant to-day; further increases of knowledge may necessitate its revision.

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* *E. nigrum* forma *japonicum* forma nov. In foliis angustissimis linearibus acutis, plerumque reflexis, a typo differt.

The case of plant C is in many respects similar to that of the preceding. The hairiness and berry colour ally it closely to *E. rubrum*. It does, however, differ from this plant in the pale translucent red of the berries and in the constantly very small leaves. Too much importance must not be attached to this latter character, since leaf-size is variable and specimens of *E. nigrum* are also known with very small leaves. Plant C therefore appears to have two small points of distinction from *E. rubrum* proper—first, the shade of the berries, and secondly, the leaf-shape, as well as a difference in habit. These differences are certainly of rather more importance and of greater degree than the difference between *E. rubrum* and its variety *atropurpureum*, so that this latter and C can scarcely be given the same taxonomic rank. The geographical facts are also slightly different in the case of C. It was originally described as a species, and was supposed to occur only in eastern North America, completely segregated from the southern red-berried plant. It is now very doubtful if this is so. In 1917, Skottsberg found, on Masafuera, Juan Fernandez, a single plant of *Empetrum*. This is unfortunately barren, but in vegetative characters it is absolutely similar to the plant from north-eastern America. Secondly, there is, in the Upsala Herbarium, a sheet with three specimens from a locality on the eastern coast of Tierra del Fuego. These are rather more hairy, but in every other respect are similar to plant C from the north. Moreover they are fruiting specimens, and to all appearances produced the pale red berries of the northern plant. These records show that there is considerable evidence for the occurrence of plant C in the south as well as in the north, and in the circumstances the geographical segregation of the northern element is not of very great significance. The conclusion is that taxonomically plant C must be considered of greater value than plant D, but not of the specific importance shown by *E. nigrum* and *E. rubrum*. It is also clearly more closely related to the latter. As a practical expression of these facts plant C is here treated as a subspecies of *E. rubrum*. Retaining the name originally assigned to it, it is here called *E. rubrum* subsp. *Eamesii*.

The three plants H, K, and L now remain to be discussed. The first of these is the glabrous red-berried form of the south, mentioned on page 509. It is clearly but a glabrous condition of *E. rubrum*. The extreme condition is somewhat rare, and there are all grades between it and the ordinary *E. rubrum*. The plant must be treated as a form of that species. It was apparently to such a plant that the name *andinum* was originally applied, and the plant may therefore now be called *E. rubrum* forma *andinum*. Its geographical range is uncertain, but the most marked specimens are found on the Chilean side of the Andes and do not seem to occur commonly in the extreme south of the continent.

Plant K is again clearly very close to *E. rubrum*, but differs in the habit and leaf-shape. The habit is open, with long branches which tend to be circinately curled at the tip. The leaves are remarkable in being narrower at the tip and distinctly apiculate. These features are sometimes very marked and the plant is very distinct at a superficial glance, but there are also all possible intergrades between it and the ordinary *E. rubrum*. It appears to be confined to the island group of Tristan da Cunha. It has been described as a species, *medium*, but there is no doubt that it is little more than a form of *E. rubrum*, and may be called *E. rubrum* forma *medium*.

The last plant to be considered is that described as L. Here, again, is another close relative of *E. rubrum*, the differences in this case being chiefly those of habit. This plant is the only one in the genus which has a true cushion habit. The branches are short and numerous, and the whole plant cushion may be of considerable size. Associated with this habit is usually a broadening of the leaves apically and an increased degree of hairiness. The extreme condition is rather common in certain localities, but there are also various intermediate conditions connecting this plant and *E. rubrum* proper. It is particularly abundant and characteristic in the Falkland Islands and is apparently almost confined to that locality. The only other records are a very few from the mountains of S. America and the islands of Cape Horn. The plant is best considered as an additional form of *E. rubrum*, to which may be applied the name *E. rubrum* forma *falklandicum* *. According to the type-specimen quoted it was upon such a plant that Gandoger based his species *E. Maclovianum*, of which the original description is most inadequate.

The relation between the plants described is seen in the clavis on page 518. The genus will be seen to comprise two species, one subspecies, one variety, and six forms. Pre-existing names have as far as possible been used in order to minimise changes in nomenclature.

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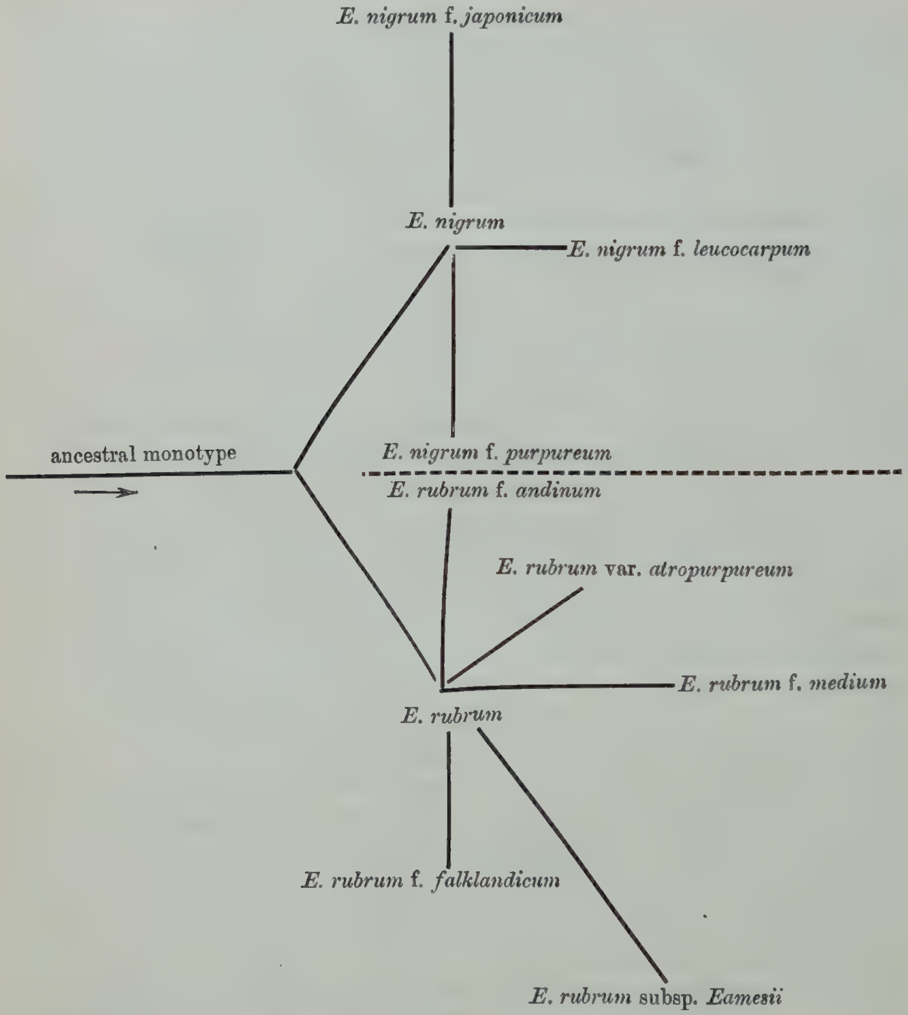
* *E. rubrum* Vahl forma *falklandicum* forma nov. In habitu pulviforme et foliis subspathulatis hirsutissimis a typo differt. Antarctic Regions, Dr. J. D. Hooker, in Herb. Mus. Brit.



Diagrammatic representation of the intra-generic relationships in *Empetrum*.

### CLAVIS.

| | |
|---|---|
| a. Berries normally black, branches glabrous .. | E. NIGRUM L. |
| b. Leaves very narrow, reflexed.......... | form. japonicum R. Good |
| bb. Leaves broad, not very reflexed. | |
| * Berries red ...................... | form. purpureum (Raf.) R. Good |
| ** Berries white ............ ...... | form. leucocarpum Asch. & Mag. |
| aa. Berries red or purple, branches normally hairy. | E. RUBRUM Vahl |
| c. Berries pale red, leaves small ........ | subsp. Eamesii (Fern. & Wieg.) [R. Good |
| cc. Berries purple ...................... | var. atropurpureum (Fern. & Wieg.) [R. Good |
| ccc. Berries opaque red. | |
| * Branches hairy. | |
| d. Leaves broadest towards the apex. | form. falklandicum R. Good |
| dd. Leaves apiculate .............. | form. medium (Carm.) R. Good |
| ** Branches glabrous ................ | form. andinum (Phil.) R. Good |

## SYNONYMY OF EMPETRUM.

- E. nigrum L.
    - *E. procumbens* Gilibert, Exercit. ii. 393.
    - *E. scoticum* Hook. Brit. Flora, ed. 2, p. 431.
    - *E. crassifolium* Raf. New Flor. Am. iii. 51.
    - *E. nigrum* var. *alpinum* Beauverd, Bull. Soc. Fr. exch. Pl. p. 47, 1919.
    - *E. nigrum* var. *loiseluriforme* Borbas, see Ung. Bot. Bl. 1908, p. 247.
    - *E. nigrum* f. *leucandra* auct.
    - *E. nigrum* f. *chlorantha* Neum. Sver. Fl. p. 292.
    - *E. nigrum* f. *hemaphrodita* auctt.
    - *E. nigrum* f. *monoica* auctt.
    - *E. nigrum* f. *dioica* auctt.
- E. nigrum f. japonicum R. Good
- E. nigrum f. purpureum (Raf.) R. Good
    - *E. purpureum* Raf. New Fl. Am. iii. 51.
    - *E. rubrum* Durand, Proc. Acad. Sci. Phil. 1863.
- E. nigrum f. leucocarpum Asch. & Mag.
- E. rubrum Vahl
- E. rubrum f. andinum (Phil.) R. Good
    - *E. andinum* Phil. ex DC. Prod. xvi. i. 26.
    - *E. rubrum* var. *andinum* DC. Prod. xvi. i. 26.
- E. rubrum f. medium (Carm.) R. Good
    - *E. medium* Carm. Trans. Linn. Soc. xii. 508.
- E. rubrum f. falklandicum R. Good
    - *E. Maclovianum* Gandoger, Bull. Soc. Bot. Fr. lx. 26.
- E. rubrum var. atropurpureum (Fern. & Wieg.) R. Good
    - *E. atropurpureum* Fern. & Wieg. Rhodora, xv. 213.
    - *E. nigrum* var. *andinum* Fern. Rhod. iv. 150, p. p.
- E. rubrum subsp. Eamesii (Fern. & Wieg.) R. Good
    - *E. Eamesii* Fern. & Wieg. Rhodora, xv. 213.
    - *E. rubrum* La Pylaie, Voyage . . . . Terre Neuve, 6. 10.
    - *E. purpureum* Raf. New Fl. Am. iii. 51, p. p.
    - *E. nigrum* var. *purpureum* DC. Prod. xvi. i. 26.
    - *E. nigrum* var. *andinum* Fern. Rhodora, iv. 150, p. p.

The following plants to which the name *Empetrum* has been applied do not belong to that genus:—

*E. acetosum* Rumph. = Begonia sp.
*E. aciculare* Bertol. = Ceratiola sp.
*E. Conradii* Torrey = Corema sp.
*E. pinnatum* Lam. = Margyricarpus sp.
*E. serrulatum* Pritz. = Empleurum sp.
*E. bilobum* Phil. = Epipetrum sp.

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The present investigation was undertaken with the main object of discovering the amount of information as to the constitution of a small plant-group which could be obtained by a careful and detailed study of an unusually extensive series of herbarium specimens, or, expressing it rather differently, to discover the possibilities of herbarium taxonomy under the most advantageous conditions. The result of the work from this point of view is epitomized in the classification of the genus given above. In the course of the work a number of problems presented themselves.

One of the first and most noticeable facts was that the individuals of the genus could very easily be separated into a comparatively small number of groups. These, it was found, had nearly all been noticed by previous workers, and it soon became clear that it was upon these groups that the taxonomy of the genus must depend and that any attempt to increase or decrease the number of such groups would be unsound. The immediate problem, therefore, became one of estimating the degree of relationship between these (10) groups.

It was quite clear that the differences between them were of very diverse magnitude and that it was impossible to give all the groups the same taxonomic value. In other words, the genus could not be considered to contain ten species. It was thus necessary to decide how the genus could be primarily divided into the least number of sections. It was then found that of the ten groups, four formed one distinct section and six formed another. Each section was then treated as comprising a single species and its subordinate variants. In reaching this conclusion it was necessary to weigh a great many considerations, most of which have been mentioned above.

The next problem was to place the groups in their right positions under the two species, and this proved to be of some difficulty. One group of each species corresponded exactly either with the original description or with the actual type-specimen of the species, and could thus be looked upon as the true species in its most typical state. The other groups had all to be treated as varyingly atypical conditions. As stated above, the differences between these groups varied very much, but were always composed of differences belonging to one or more of three kinds: first, difference due to a single continuously variable character; second, difference due to a single discontinuously variable character, and third, difference of geographical range. The first and second kinds were of most importance and the third was used mainly to intensify the others. In general the principle adopted was to give to groups differing least from the actual species the least taxonomic rank and to increase the rank proportionally to the increase of difference.

One other point of considerable theoretical interest remains to be mentioned. This is the question of the relation between *E. nigrum* forma *purpureum* and *E. rubrum* forma *andinum*. It will be noticed that in the diagram of the genus they are placed close together but under different species. It is true that there is a very slight difference of habit, but if this, which may well be due to habitat, is ignored, the plants are apparently identical. At the same time, on the evidence available it is inevitable to consider them as specifically distinct. It is probable that such a case is rare in such simplicity, but even so it raises very important considerations as to the value, from the taxonomic point of view, of external resemblance. It is emphasized here as a phenomenon which must be taken into account in all taxonomic work.

## SUMMARY.

1. The family Empetraceæ is described and its position in a natural classification is discussed. According to the consensus of modern opinion its proper place is either next the Ericaceæ or as an additional tribe within that family.

2. The biology of the genus *Empetrum* is described.

3. Its geographical distribution is described in detail and the most important ecological features are noticed briefly.

4. Variation within the genus is described and is shown to be chiefly in seven characters :—general habit, degree of hairiness, shape and size of leaf, arrangement of leaves, angle of leaf-insertion, sex of flowers, colour of berry.

5. The morphological and geographical range of each of these seven characters is described in detail.

6. Variation as seen in these characters is of three kinds : simple continuous, complex continuous, and discontinuous.

7. It is shown that instead of an almost indefinite number of forms within the genus all the individuals fall into ten clearly differentiated groups. This is chiefly due to the combined influence of correlated variation and geographical segregation.

8. These ten groups are described.

9. Previous taxonomic work on the genus is briefly reviewed.

10. The inter-relationships of the ten groups comprising the genus are fully discussed and a taxonomic treatment is suggested, which is, in the writer's opinion, expressive of the conclusions reached in the discussion.

11. According to this classification the genus contains two species, one having a subspecies, a variety and three forms, the other having three forms.

12. In conclusion the methods adopted in the taxonomic treatment are described and discussed.

The writer gratefully acknowledges his deep indebtedness to the Directors of the Herbaria at Berlin, Upsala, Geneva, Copenhagen, Leningrad, and the Gray Herbarium for the loan of numerous specimens by which the detailed analysis of the genus was made possible. His thanks are also due to many friends who have offered valuable criticisms, advice and information, and to the Librarian of the Botanical Department of the British Museum (Nat. Hist.) for his help with the extensive literature of the genus.

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# The Genus *Lilæopsis* : a Study in Geographical Distribution.

By A. W. Hill, C.M.G., F.R.S., F.L.S.

(Plates 19 & 20 and 16 Text-figures.)

[Read 6th May, 1926.]

Under the name *Crantzia lineata*, Nuttall described a small Umbelliferous plant found in swampy districts in New Jersey, North America. Subsequently F. Mueller described an Australian specimen under the name *C. australica* ; Hooker and Arnott described *C. attenuata* on specimens from Buenos Aires, and Schlechter described a fourth species, *C. Schaffneriana*, on a specimen collected by Schaffner near Mexico City. In the 'Index Kewensis,' owing no doubt to the inadequate descriptions and to the general similarity of the vegetative characters of the specimens, these three species were referred to *C. lineata* Nutt.

The earliest specimen of a *Crantzia* bearing a specific name is, however, to be found in the Linnean Herbarium, for Linné's *Hydrocotyle chinensis* proves to be Nuttall's *Crantzia lineata* from Eastern North America. Why the locality China was assumed for this specimen does not appear, but the identity of this plant with the original *C. lineata* unfortunately necessitates the adoption of the specific name *chinensis* for the E. North American species, as has been pointed out by O. Kuntze (Rev. Gen. Plant. iii. p. 114) *.

In the year 1891 Greene gave the name *Lilæopsis* † to the Umbelliferous genus *Crantzia*, since there were three early genera bearing the name *Crantzia*, one of which, *Crantzia* Sw. (1788), is retained for a genus allied to *Buxus*. Coulter and Rose ‡, in 1897, worked through the North American specimens, and they maintained Nuttall's species *lineata* as they had not seen the Linnean specimen, and also described *L. occidentalis* from Western North America and *L. carolinensis* from Carolina and Louisiana. They retained Schlechtendal's Mexican species as *Lilæopsis Schaffneriana*, and included under it specimens from Arizona as well as one from Southern Chile.

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* According to Fernald (Rhodora, xxvi. 1924, p. 93), Asa Gray examined the Linnean type of *Hydrocotyle chinensis*, and did not consider it was the N. American *C. lineata*, but from a careful examination of the specimen, I find it agrees closely with the Virginian material.

† 'Pittonia,' ii. p. 192 (1891). Coulter & Rose, "North American Umbelliferæ": Contributions from the National Herbarium, vii. p. 123.

‡ Bot. Gaz. xxiv. p. 48, 1897, figs. 2 & 4.

These authors also suggested that the Australian and Brazilian specimens which have been referred to *Crantzia lineata* probably represented two distinct species, but they did not attempt to define them.

Gandoger, in 1918, described three new species of *Crantzia*—*C. macloviana, C. Novæ-Zelandiæ,* and *C. polyantha*—in Bull. Soc. Bot. France, lxv. p. 31. The first, founded on Skottsberg's No. 101 from the Falkland Islands, he distinguishes from the other species (which include also *C. lineata* Nutt.), by the single and valueless character of "Styli recti."

Monsieur Gandoger kindly sent me his specimens for examination. His species *C. polyantha* proved to be identical with F. Mueller's *C. australica*, and *C. Novæ-Zelandiæ*—of which the sole description is "umbella 2–3-flora, foliis saltem triplo brevior," in contrast to "umbella 6–8-flora" (*C. polyantha* and *C. lineata*)—is the same as the specimens which I was proposing to name after Bidwill, the collector, on ample fruiting material at Kew and the British Museum. This must now be named *L. novæ-zelandiæ* (Gandog.) A. W. Hill.

Specimens are now to be found in various herbaria referred to *Crantzia lineata* Nutt., which have been collected in New Zealand, Australia, Tasmania, the Falklands, South Georgia, Chile, the Argentine, Uruguay, Paraguay, Brazil, the Andes of Bolivia and Peru, Ecuador, Colombia, Mexico, and in Eastern and Western North America as far north as Alaska.

Except in the cases of the true *Lilæopsis chinensis* (*L. lineata*), from the South-Eastern United States and some specimens from Eastern South America with spathulate "leaves," which prove to be *L. carolinensis* Coult. & Rose, it is hardly possible to assign the specimens from these widely diverse localities to separate species on their macroscopic vegetative characters.

If, however, the fruits of the different specimens are compared and are studied by means of transverse sections, it becomes evident that the genus *Lilæopsis* contains several distinct species.

Unfortunately, some of the specimens have been collected only in flower or with immature fruits; it is not possible, therefore, to submit a complete revision of the genus, and it is to be hoped that collectors may be induced, in the future, to pay more attention to these inconspicuous little plants which frequent damp and marshy places, and so enable a better knowledge to be obtained of this widespread genus, whose species possess so similar a general facies.

Judging from the structure of the fruits, and comparing them with what we know of the fruit structure of other genera of Umbelliferæ, it seems possible that the plants placed in the genus *Crantzia* by the earlier botanists, might be referred to more than one genus; but owing to the adoption of a similar habitat, the representatives have assumed, through reduction, so similar a vegetative habit, that it seems best to regard them as belonging to a single genus, No attempt will be made to enlarge on this suggestion in these pages beyond pointing out that the structure of the fruit shown by *L. chinensis* (*L. lineata*) and the species from the Falklands, the Andes, from Southern Chile and from Bass Strait, Australia, is of so different a type from that shown on the one hand by the fruits of *L. Schaffneriana* and of the species from Ecuador and the Argentine, and on the other hand by the fruit of the striking Australian species, *L. fistulosa* (Caley MS.) A. W. Hill, that were there any marked foliar or floral characters they would probably be referred to three distinct genera.

The specimens of this genus preserved in the Herbaria at Kew, the British Museum, the Linnean Society, Cambridge, Edinburgh, Paris, Stockholm, Upsala, the Boissier Herbarium, the United States National Museum, and the Gray Herbarium, Harvard University, as well as those in M. Gandoger's Herbarium, have been examined and compared, and there appear to be some fourteen distinct species, generally restricted to well-marked geographical areas. There are probably one or two more in Southern Chile, New Zealand, and Australia which are represented at present only by imperfect specimens in herbaria.

In general habit the plants are of a tufted character with rosettes of "leaves," especially in the more alpine forms, and long, creeping rhizomes, which bear single "leaves" or small leafy shoots and inflorescences at the nodes, whence also the roots are produced.

The fistulose "leaves" have broad sheathing bases, and either terminate in points like an awl or are more or less spathulate (cf. *L. chinensis* (L.) Kuntze and *L. carolinensis* Coult. & Rose), and when pressed show transverse septa. The number of these septa does not bear any definite relation to the size of the leaf, but they appear to be fairly constant, for some of the species with the shortest "leaves" often show the greatest number of septa *. Bentham and Hooker † suggest that these septate cylindrical leaves, which are similar to those of *Ottoa œnanthoides* Kunth, are in reality phyllodes; a view which is supported by a lacustrine form from Rotokakahi, New Zealand (*L. lacustris* A. W. Hill), which shows in one or two cases either a single leaflet or a pair of leaflets at most of the septa of the "leaf" or rather phyllode, as I prefer to regard the leafy organ (text-fig. 1, p. 528).

Goebel ('Organography of Plants,' Eng. Ed. pt. ii. p. 295), gives a figure (fig. 193), of a young leaf of a New Zealand specimen of "*Crantzia linearis*," which may probably be my *L. lacustris*, showing what he thinks may be arrested primordia or leaf-pinnules. These, though produced only in one row, resemble closely the "leaflets" shown on the New Zealand specimen preserved at Kew, and add support to the view that the leaves of *Lilæopsis* are reduced to petiole and rachis only. It may be mentioned here that the orientation of the vascular bundles supports the view that the leafy organs are of the nature of phyllodes.

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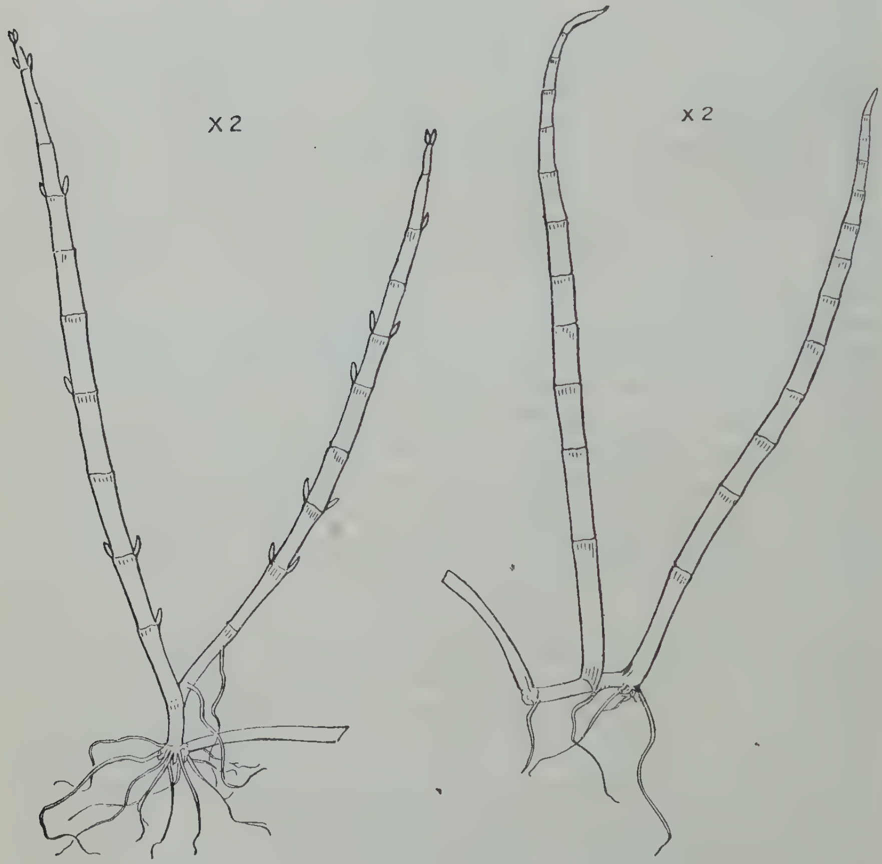
* *L. andina* A. W. Hill, where the leaves are 1–2·5 cm. long with 9–13 septa, and *L. carolinensis*, from Buenos Aires, where the leaves are as much as 15 cm. long and show some 6–10 septa.

† Bentham & Hooker, Gen. Plant. i. p. 906. *Cf.* Coulter & Rose, Bot. Gaz. xxiv. p. 48 (1897).

Briquet (Bull. Herb. Boiss. v. 1897, p. 455) has studied the septate leaves of *Ottoa œnanthoides* Kunth, a plant inhabiting marshes in Colombia and Mexico, which closely resemble those of *Lilæopsis* (*Crantzia*), as do also the leaves of *Tiedmannia* (*Peucedanum*) *teretifolia* DC., and has compared both with the leaves of *Lilæopsis* (Briquet, *l. c.* pp. 459 & 465).

TEXT-FIG. 1.



*L. lacustris* A. W. Hill.

He concludes that as the leaf of *Lilæopsis* consists of a sheath, petiole, and septate rachis it is not a true phyllode, which should consist of sheath and petiole only. The discovery of the New Zealand specimen with leaflets attached, borne at the septa, may perhaps be held to support Briquet's view.

It does, however, seem clear, whatever view one may hold as to the exact morphological value of a phyllode, that the so-called "leaves" of *Lilæopsis* as well as those of *Ottoa* are reduced to sheath and petiole only, or that the petiole is prolonged imperceptibly into the septate rachis. Leaves of *Crantzia lineata* are also figured by Bitter (Flora, lxxxiii. 1897, p. 272), and the characteristic septa and parallel veins are well shown.

The umbels are in all cases simple, but they vary considerably in their relation to the length of the leaves in the different species, the original species, *L. chinensis* (*C. lineata*), being the only one in which the umbels exceed the leaves in length. The number of flowers varies from two to about twelve, and the pedicels are occasionally of some length and sometimes pendulous; the involucral bracts are variable in size and number, but are usually very few and small. The fruits vary in size and are distinctly longer than broad in some species (this is remarkably the case in *L. fistulosa* A. W. Hill), and the reverse in others; in some of the species the two mericarps do not appear to separate when ripe (*L. macloviana* etc.). The prominence of the dorsal ribs and the nature of the lateral ribs considerably affect the external appearance of the fruits, and on this character the species can be arranged into two more or less natural groups. It is in transverse sections of the ripe fruits that these characters are particularly noticeable, and the two types of fruit can be readily recognized (see Plates **19** & **20**).

As Briquet has pointed out, the patches of lignified tissue which are prominent features in the transverse sections of the fruit are provisions for floating, correlated with the aquatic environment of these plants.

The fruit as seen in transverse section agrees with the fruits of the allied genera of the sub-group Apioideæ (Drude). It is usually almost spherical or slightly compressed laterally. Each mericarp shows three or five primary ribs with usually a single oil-duct or vitta, in each of the grooves and two at the commissure, but in some species there may be 4–6 ducts at the commissure, and a similar multiplication of the ducts may be found in the grooves (*L. Brownii*). The character of the ribs and the number and distribution of the oil-ducts afford useful and, I believe, reliable specific characters.

In some of the species, forming one definite group, the two lateral ribs only are prominent, and are composed of comparatively large lignified cells, the three dorsal ribs remaining small, whilst the species which form the other group have all the five ribs composed of angular masses of lignified tissue and give the fruit a conspicuously ribbed appearance.

Coulter and Rose have recognized these two types of fruit in the specimens they have described and figured.

The plants grow normally in swampy or damp sandy places by the shores of rivers and lakes, or by the sea, and sometimes are found partly submerged. Under the latter conditions the "leaves" are usually elongated and flowers are sparingly produced, and the whole vegetative appearance of the plant is much changed. *L. carolinensis* Coult. & Rose, affords a good example of the different appearance of this species in accordance with its habitat, and similar alterations are shown by *L. andina* A. W. Hill, when growing on land or partly under water *. *L. tenuis* A. W. Hill, from Brazil, which grows in a swamp, has become almost like an alga with delicate, filamentous rhizomes and leaves (see text-fig. 6, p. 540).

It will be useful at this point to tabulate all the known and proposed species of *Lilæopsis* under their respective sub-groups as determined mainly by an examination of transverse sections of the fruits.

A.—Fruit with all five ribs prominent and angular and composed of lignified cells.

| | |
|---|---|
| *L. chinensis* (L.) Kuntze. | E. N. America, Massachusetts to Florida. |
| *L. carolinensis* Coult. & Rose. | S.E. United States, Argentine, and Eastern S. America to Brazil. |
| *L. Schaffneriana* (Schlecht.) Coult. & Rose. | Mexico and Ecuador. |
| *L. recurva* A. W. Hill. | Arizona. |
| *L. australica* A. W. Hill. | Australia, Victoria. |
| *L. fistulosa* A. W. Hill †. | Australia, New South Wales. |

B.—Fruit with only the two lateral ribs prominently thickened and composed of lignified cells. Dorsal ribs without lignified cells and generally rounded and inconspicuous.

| | |
|---|---|
| *L. macloviana* (Gandog.) A. W. Hill. | Falkland Islands and Patagonia. |
| *L. sinuata* A. W. Hill. | S. America, Chiloe and Valdivia, S. Chile. |
| *L. Brownii* A. W. Hill. | Tasmania, Kent's Group, Bass Strait. |
| *L. occidentalis* Coult. & Rose. | W. N. America, Alaska, Vancouver to California. |
| *L. andina* A. W. Hill. | Andes of Peru, Bolivia, and Chile. |
| *L. novæ-zelandiæ* (Gandog.) A. W. Hill. | New Zealand, South Island. |
| *L. lacustris* A. W. Hill. | New Zealand, North Island. |

C.—Fruits with delicate thin ribs, cells not lignified.

| | |
|---|---|
| *L. tenuis* A. W. Hill ‡. | Brazil, Parana. |

A few specimens cannot be named, as, unfortunately, they bear neither fruits nor flowers; one from South Georgia may represent a distinct species allied to *L. macloviana*, and another collected by Mrs. A. Dietrich

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* Chodat, in Bull. Soc. Bot. Genève, sér. 2, xii. 1920, pp. 28-30, discusses the various biological forms assumed by the species of *Lilæopsis* (*Crantzia*), and refers particularly to Mandon's specimens from Bolivia. See Weddell, Chlor. And., Tab. 68 & 69.

† Though the fruits of *L. fistulosa* possess five prominent ribs, the fruit structure is so unlike that of any other species that it should probably be placed in a class by itself.

‡ *L. tenuis* is also difficult to place as the delicate fruit is not very comparable to that of any other species.

"near Brisbane River, Australia," which has been referred to "*Crantzia australica* Muell.," in the 'Flora Australiensis.'

The sections of the fruits, taken from Herbarium specimens, have been cut by Mr. L. A. Boodle, and I am much indebted to him for his assistance, as the task presented considerable difficulties owing to the age and dry condition of the material.

The microphotographs of the fruit sections have most kindly been made by Dr. G. H. Rodman, of Putney, who, as is well known, has devoted his leisure time to photomicrographic work and botanical studies. Considering the nature of the material, his results have been very successful. I am greatly indebted to him for his valuable help.

## LILÆOPSIS.

### *Key to the Species.*

| | | |
|---|---|---|
| 1. | Leaves distinctly spathulate, peduncles longer or shorter than the leaves | 2. |
| | Leaves cylindrical, linear or filiform, terete, peduncles shorter than the leaves | 3. |
| 2. | Peduncles longer than the leaves, fruits with the two lateral ribs well-developed; vittæ 6–7 | (1) *L. chinensis* (*lineata*). |
| | Peduncles shorter than the leaves, fruits with all the ribs prominently-developed and angular; vittæ 6, rarely 8–10. | (4) *L. carolinensis.* |
| 3. | Fruits delicate, about twice as long as broad, ribs inconspicuous; vittæ 6. Leaves very slender, filiform and alga-like | (6) *L. tenuis.* |
| | Fruits large, nearly twice as long as broad, with five conspicuous angular ribs; vittæ 6. Leaves stout, up to 30 cm. long | (12) *L. fistulosa.* |
| | Fruits more or less orbicular. Leaves linear or filiform, somewhat coriaceous | 4. |
| 4. | Fruits with all five ribs prominently-developed, often strengthened by bars of sclerous cells | 5. |
| | Fruits with only two lateral ribs prominent, composed of large lignified cells, the dorsal ribs rounded or only slightly projecting | 7. |
| 5. | Fruit ribs rounded without sclerous patches; vittæ 6–8, pedicels recurved | (3) *L. recurva.* |
| | Fruit ribs angular acute with sclerous patches; vittæ 6 or 8–9, pedicels erect | 6. |
| 6. | Fruits longer than broad; vittæ 8–9 | (11) *L. australica.* |
| | Fruits orbicular; vittæ 6 | (5) *L. Schaffneriana.* |
| 7. | Vittæ 13–15, two or three being between each of the ribs | (10) *L. Brownii.* |
| | Vittæ 6–10, only one between each rib and 2–6 at the commissure | 8. |

| | | |
|---|---|---|
| 8. | Lateral ribs elongated and extended laterally along the commissure | 9. |
| | Lateral ribs rounded and not laterally extended | 11. |
| 9. | Vittæ 6 | (8) *L. sinuata.* |
| | Vittæ 9–10 | 10. |
| 10. | Fruits 1–1·25 mm. broad; vittæ 10 | (7 *a*) *L. andina* var. *multivittata.* |
| | Fruits 1·75 mm. broad; vittæ 8–10 | (9) *L. macloviana.* |
| 11. | Fruits ovoid; vittæ 6–8 | 12. |
| | Fruits cylindric, twice as long as broad; vittæ 6 | (14) *L. lacustris.* |
| 12. | Lateral ribs extended somewhat laterally; vittæ 6 | (2) *L. occidentalis.* |
| | Lateral ribs extended somewhat laterally; dorsal ribs distinct, subacute; vittæ 8 | (13) *L. novæ-zelandiæ.* |
| | Lateral ribs extended somewhat dorsally; dorsal ribs inconspicuous, rounded; vittæ 6, sometimes 8 | (7) *L. andina.* |

1. **Lilæopsis chinensis** (*L.*) *Kuntze,* Rev. Gen. Plant. iii. p. 114 (1898).

*Hydrocotyle chinensis* Linn. Sp. Pl. No. 5, p. 234 (1753); Spreng. in Roem. & Schultes, Syst. Veg. vi. p. 355.

*Hydrocotyle lineata* Michx. Fl. Bor.-Amer. i. p. 162 (1803); Richard, Monogr. Hydr. p. 77, fig. 38.

*Hydrocotyle ligulata* Bosc, ex DC. Prod. iv. p. 71.

*Crantzia lineata* Nutt. Gen. Plant. Am. i. p. 177 (1818); DC. Prod. iv. p. 71; Torr. et Gray, Fl. Am. Bor. ii. p. 600.

*Lilæopsis lineata* (Michx.) Greene, Pittonia, ii. p. 192 (1891); Coulter & Rose, N. Amer. Umbellif. p. 123, fig. 36; Bot. Gaz. xxiv. p. 47 (1897); Britt. & Brown, Ill. Fl. N. U. States and Canada, ii. p. 521 (ed. 2, p. 648); Fernald, Rhodora, xxiii. p. 110 (1921), and xxvi. p. 93 (1924).

*Hallomuellera lineata* Kuntze, Rev. Gen. Pl. i. p. 267 (1891).

(Descr. ampl.) *Fructus* ovoideus vel turbinatus, 1·75 mm. longus, 2 mm. latus, costis dorsalibus minutis acutis, lateralibus rotundatis conspicuis; vittæ plerumque 6 vel rarius 7, quarum 2 vel 3 commissurales. (Plate **20**. fig. 8.)

NOVA SCOTIA. Yarmouth County: Tusket River; among bases of *Spartina alterniflora, Fernald & Linder* 22067.

MAINE. Woolwich: Black River Creek; "forming close turf over extensive areas of salt marsh," *Fernald & Long* 252.

MASSACHUSETTS. Barnstaple County: Bass River; Yarmouth, *Fernald & Long* 18874; Bourne, abundant under *Spartina, Farlow*; Wareham, *Kennedy*; Ipswich River, *Sears*; Newmarket, Adams Point, *Eaton* 210.

CONNECTICUT. Milford; "abundant in parts of Housatonic River with *Spartina* sp. etc. mostly submerged at each high tide," *Dr. E. H. Eames*; banks of the Housatonic River, *Dr. Torrey.*

New Jersey. Cape May Co.: Palermo; salt marsh, *Long & Van Pelt*; New Jersey, *Nuttall*; Providence, *J. W. Congdon*; Providence, Rhode Island, *S. T. Olney* in Herb. Kew.; New Jersey, *Dr. Torrey*; New Pine Barrens, *Dr. & Mrs. Britton* & *Wilson* (July 1900); New Jersey, salt marsh near Egg Harbour, *Nuttall* in Herb. Mus. Brit.

Maryland. Kent County; Chester River cliffs landing, *Forrest Shreve* 1094; mouth of Little Gunpowder River, *G. H. Shull* 297.

Virginia. Queen's Creek; tidal marsh, *E. J. Grimes* 3063; near Norfolk, swampy places near sea, *Rugel* (June 1840) in Herb. Mus. Brit. et Edin.; Virginia, *Mitchell*.

"*Elatine Hydropiper* Herb. Gronov." Fl. Virg. 3, p. 62 (quoted erroneously by Linn. Sp. Pl. 367 as a synonym of *Elatine Hydropiper*), *Clayton* in Herb. Mus. Brit.

Georgia. Liberty County: North Newport River; near Riceboro, brackish marshes, *R. M. Harper* 2182.

Florida. Tampa, *Dr. Garber* (1876); ex herb. *J. Torrey*; nr. Jacksonville, shore of St. John's River, *A. H. Curtiss* 993; Florida, banks of St. John's River near Jacksonville, *A. H. Curtiss*; Florida, *Chapman* in Herb. Kew. et Herb. Edin.; Florida, *Curtiss* 4915; Florida, *Herb. A. Gray* in Herb. Mus. Brit.; salt marshes, Brighton, *T. Nuttall & B. D. Greene* (July 1840) in Mus. Bot. Upsala.

The Linnean specimen of *Hydrocotyle chinensis* has been compared with numerous specimens of *Crantzia lineata* Nutt. from N. America, including Nuttall's type at the British Museum, and it is certainly the true Eastern N. American species. For some unknown reason the locality of the specimen has been given as China; but there is no evidence for this, nor is any locality given on the sheet in the Linnean Herbarium. All that is written on the sheet is on the back in Linnæus's handwriting:—"646 Hydrocotyle fol. brevibus linearibus integris obtusis, radice repente. *Gron.*"

This same description, "*radice repente*" being altered to "*radice reptatrice*," occurs in Gronovius's Fl. Virg. (1739), p. 158, and in Ed. 2 (1762), p. 62, where it is put as a synonym of *Elatine foliis oppositis* Linn.; and to this entry Linnæus has made a MS. marginal note, "*Hydropiper*," in the Linnean copy of the 'Flora.' It is unnecessary, therefore, to follow Gronovius further in this erroneous citation. It is, however, unfortunately necessary to take up the specific name *chinensis* for Nuttall's *Crantzia lineata*.

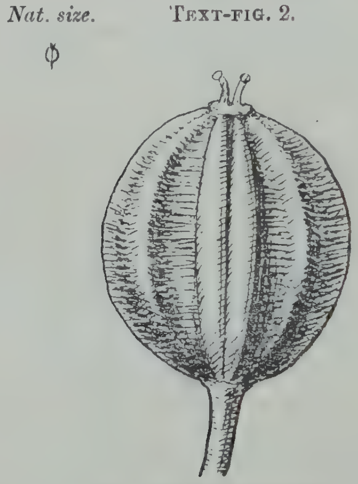
Kuntze, in making the combination which is here adopted, gives "Argentina" and "Cordoba" as localities for *L. chinensis*, and so adds a further geographical error, since this well-marked species has been recorded only from the Eastern States of N. America.

Coulter and Rose give a figure of the fruit-section of *L. lineata* showing four vittæ at the commissure of each mericarp, though no mention of this character is made in the description. I have examined several fruit-sections from different specimens, and find that two vittæ at the commissure is the normal occurrence, though occasionally there may be three, two on one side and one on the other, owing to the division of one of the vittæ.

2. **Lilæopsis occidentalis** *Coulter & Rose* in Bot. Gaz. xxiv. p. 48, fig. 2 (1897); N. Amer. Umbellif. p. 124, fig. 37.

(Descr. ampl.) *Folia* 4–13 cm. longa. *Umbella* 5–10-flora. *Fructus* ovoideus, 1–5 mm. longus, 1·25 mm. latus, costis dorsalibus minutis acutis, lateralibus conspicuis; vittæ 6, quarum 2 commissurales. (Plate **20**. fig. 4.)

TEXT-FIG. 2.



*L. occidentalis* Coulter & Rose. × 20.

ALASKA. *T. Meehan* (July 1883) in Herb. Edin.

BRITISH COLUMBIA. Vancouver Island; near Comox (July 1, 1893), *J. Macoun* 307 in Herb. Kew. et Mus. Brit.; Alberni, along the beach (June 25, 1907), *Rosendahl* 1918; Vancouver Island, Nanaimo, *Macoun* 78, 625, 78, 824; Alberni, salt marsh, *J. K. Henry* 9055.

WASHINGTON. King Co.; gravelly shore of Lake Washington, *Suksdorf* 972; Seattle, *C. V. Piper* 642; Gray's Harbour, tide-flats, marsh along coast, *A. S. Foster* 882; Western Washington, Chehalis County, *F. H. Lamb* 1272 in Herb. Kew.

OREGON. Tillamook; salt marshes, *T. J. Howell* (July 1882) in Mus. Bot. Upsala et in Herb. Mus. Paris; Oregon, *Hall* 205 in Herb. Mus. Brit.; Newport, freshwater stream behind dune, *Nelson* 2321; Lighthouse point, near Astoria, *Meehan* (Aug. 1883); Tillamook Bay, salt marshes, *L. F. Henderson* 402; Roquel River, wet ground near the mouth, *M. E. Peck* 8698.

CALIFORNIA. Napa County; bank of the Napa River, *W. N. Suksdorf* 630; N. coast region of California, region about Humboldt Bay, *J. P. Tracy* 3102; mouth of Little River, *Tracy* 5391; head of Drakes Elters, Point Reyes, *Burtt Davy* 6734 & 6841 in Herb. Univ. Calif.

The Californian specimens have much narrower and more slender leaves, and are rather unlike the forms from further north. The fruits, however, agree in structure with those of the plants from Oregon and further north. I have therefore referred the Californian specimens to *L. occidentalis*.

3. **Lilæopsis recurva** *A. W. Hill.*

*Lilæopsis Schaffneriana* Coult. & Rose in Bot. Gaz. xxiv. p. 48, non Schlecht., quoad specim. Arizon.

Species *L. Schaffneriana* (Schlecht.) Coult. & Rose, affinis, sed pedicellis recurvatis, fructibus lævibus elongatis costis 5 cellularum lignosarum sine sclerenchymate compositis distincta.

*Folia* 5–24 cm. longa, 0·75–3 mm. lata. *Pedunculi* 3–4 cm. longi, 7–10-flori, pedicellis 1–1·5 cm. longis recurvis pendulis. *Fructus* 2–2·25 mm. longus, 1·25–1·5 mm. latus, cylindricus, costis rotundatis; mericarpium in sectione transversali areis 5 lignosis distinctis sine sclerenchymate instructum; vittæ 6, rarius 7–8, quarum 2 vel 3–4 commissurales. (Plate **19**. figs. 5, 6.)

N. America. S. Arizona; near Fort Huachuca (July 1882), *Lemmon* 2895 in Gray Herb.; Santa Cruz Valley, near Tucson (1881), *Pringle* in U.S. Nat. Herb. et Gray Herb.

The outer layers of cells of the mericarp in young fruits are filled with starch which prevents the collapse of the cells in dried material. In ripe fruits these outer layers are usually shrunken and empty and all the starch has disappeared. (Plate **19**. figs. 5 & 6.)

4. **Lilæopsis carolinensis** *Coulter & Rose* in Bot. Gaz. xxiv. p. 48, fig. 4 (1897); N. Amer. Umbellif. p. 124, fig. 38.

*Crantzia attenuata* Hook. & Arn. in Hook. Bot. Misc. iii. p. 346 (1833).
*Crantzia brasiliensis* Glaz. in Mém. Soc. Bot. France, 3, p. 331 (1909).
*Lilæopsis attenuata* Fernald in Rhodora, n. s. lxxii. p. 94 (1924), in adnot.
*Crantzia carolinensis* (Coult. & Rose) Chod. Bull. Soc. Bot. Genève. sér. 2, xii. p. 31 (1920).

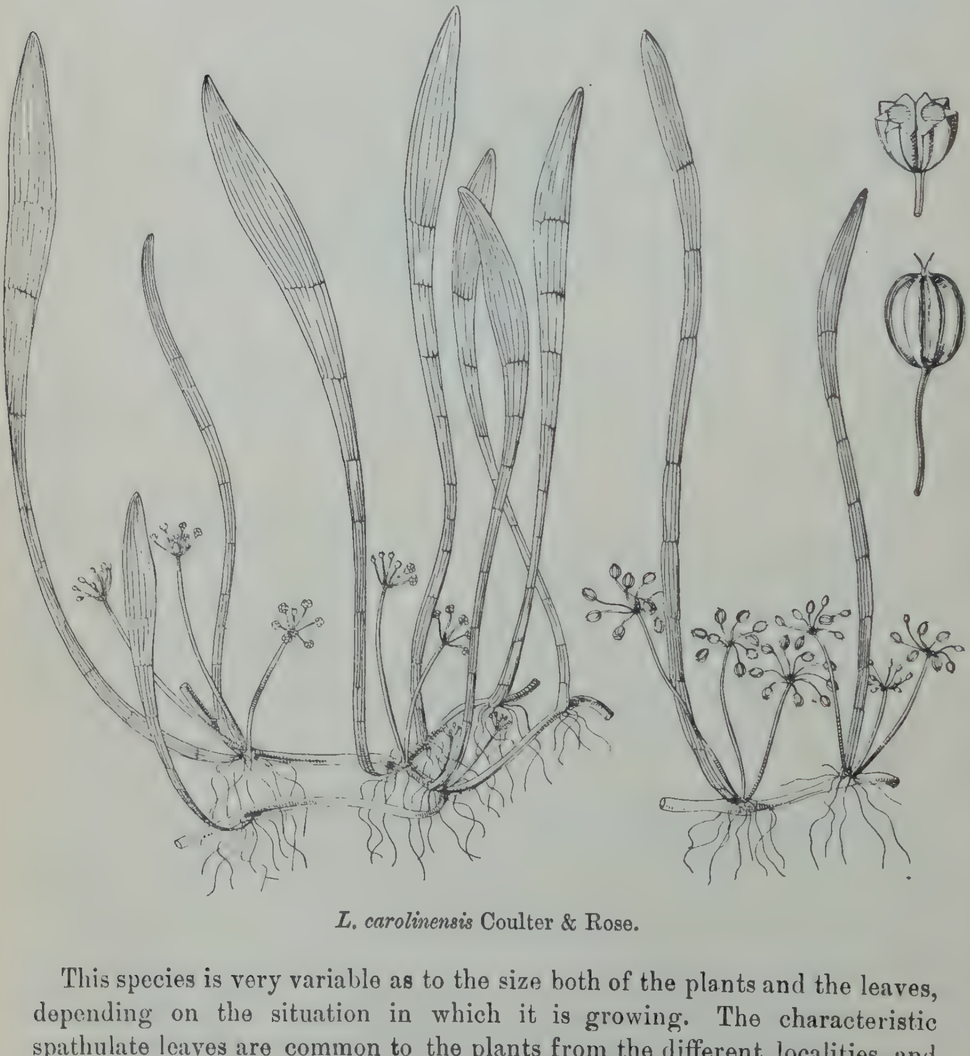
*Folia* 12–15 cm. longa, spathulata, 0·7–1 cm. lata. *Pedunculi* 1–5 cm. longi, 8–15-flori; pedicelli circiter 1 cm. longi. *Fructus* 2–2·25 mm. longus, 2 mm. latus, costis 5 lignosis sectione transversali deltoideis acutis instructus, lateralibus majoribus; vittæ plerumque 6, magnæ, quarum 2 commissurales, aliquando divisis itaque 8–10, quarum 4–5 commissurales. (Plate **19**. fig. 1.)

N. America. Eastern N. Carolina, *McCarthy* (1884) in U.S. Nat. Herb.; New Orleans, *J. F. Joor* in U.S. Nat. Herb. 318526; without locality or collector in U.S. Nat. Herb. 200130. New Orleans, floating in canals, *A. B. Langlois* (April 1883) in Herb. N. Y. Bot. Garden.

S. AMERICA. Argentine; Buenos Aires, *Tweedie* in Herb. Kew.; Concepcion del Uruguay, *Lorentz* (1878) in Herb. Kew. et Upsala.; Misiones: Belgran Nunez; near Alto Parana River, *Ekman* (1907) in Herb. Kew. et Mus. Bot. Stockh.; Uruguay, River Plate, Colonia, *Berro* 1951 in Herb. Kew.; Monte Video, Rincon del Cerro, *M. Fruchard* (June 1877) in Herb. Mus. Paris. Banda Oriental del Uruguay, Voy. *Aug. de Saint-Hilaire* 2247 in Herb. Mus. Paris.

PARAGUAY. Lake Ypacaray, *Hassler* 12271 (Sept. 1913) in Herb. Mus. Brit.

TEXT-FIG. 3.



*L. carolinensis* Coulter & Rose.

This species is very variable as to the size both of the plants and the leaves, depending on the situation in which it is growing. The characteristic spathulate leaves are common to the plants from the different localities, and the fruits, in all cases where they are mature, possess prominent ribs tipped with patches of sclerous tissue; the vittæ are large and, though normally six may be as many as ten by division. (Plate 19. fig. 1.)

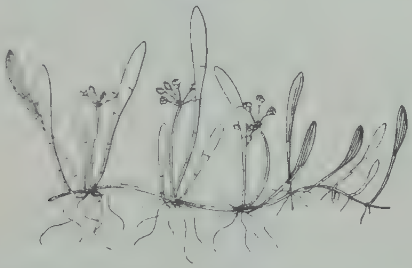
As with other species, plants living partly in the water develop much longer leaves, and in this species under such conditions they become attenuated and lose their spathulate character. Under drier conditions forms referred to the variety *minor* occur.

**L. carolinensis** var. **minor** *A. W. Hill.*

*Crantzia brasiliensis* Glaz. in Mém. Soc. Bot. France, 3, p. 331 (1909) quoad sp. Braz. Coll. Glaziou.

*Rhizoma* elongata, repens. *Folia* spathulata, 1·5–7 cm. longa, apice 1·5–4·5 mm. lata. *Umbella* 1–1·5 cm. longa. *Fructus* quam typo minor, costis dorsalibus minoribus.

TEXT-FIG. 4.



*L. carolinensis* Coulter & Rose var. *minor* A. W. Hill.

PARAGUAY. Guarapi; marshy prairies (1879), *Balansa* 3164 in Herb. Kew. et in Herb. Mus. Paris; Cerros de Tobaty, *Hassler* 6439 in Herb. Kew. et in Herb. Mus. Paris.

ARGENTINE. La Plata; tide marks, *Tweedie* in Herb. Kew. et Mus. Brit.

URUGUAY. Dep. Montevideo: Carrasco; in damp sandy places and ditches, *Corn. Osten* 5778 in U.S. Nat. Herb. 1134377; Montevideo, Lago Buceo, *Courbon* 1856 in Herb. Mus. Paris.

BRAZIL. Rio Janeiro, *Glaziou* 18510 in Herb Kew.; Minas, between Ouro Preto and Marianna (June 1884), *Glaziou* in Herb. Mus. Paris; Rio Grande do Sul: Porto Alegre; Pedras Brancas, *Lindman* A. 407 in Mus. Bot. Stock.; Rio Grande, sandy fields and marshy places, *Malme* in Mus. Bot. Stockh.

This variety is readily separated from the type by its small spathulate leaves and long creeping rhizomes. The fruits are also smaller with the dorsal ribs less pronounced.

**L. carolinensis** var. **attenuata** *A. W. Hill.*

*Crantzia attenuata* Hook. & Arn. in Hook. Bot. Misc. iii. p. 346.

*Folia* attenuata, 10–15 cm. longa, 1–2 mm. lata, acuminata. *Umbella* circiter 4 cm. longa.

Argentine. Buenos Aires, *Tweedie*; Rio Primero (1878), *Hieronymus* in Herb. Kew. et Mus. Brit. (?).

Brazil. Near Itatiaya, *Rose & Russell* 20507 in U.S. Nat. Mus. 762618 (?).

This appears to be only a varietal form of *L. carolinensis* with long linear leaves. Hooker and Arnott's description reads: " *Crantzia attenuata* Hook. et Arn. foliis elongatis attenuatis pedunculo triplo longioribus Buenos Ayres *Tweedie*," and it is said to differ from " *Crantzia linearis*," of North America, in its much longer and attenuated foliage. The long narrow leaves probably are due to the fact that this plant was growing in water, as the character of the plant, I am informed by Prof. Hauman, of Buenos Aires, is very variable, depending on the locality in which it may be growing.

On the Kew sheet bearing the name " *Crantzia attenuata*, H.A.," there are three different collections: (1) labelled " Buenos Ayres *Tweedie*", with leaves 12–15 cm. long, with long tapering points, and peduncles 3–4 cm. long; (2) a slender plant, labelled " La Plata *Tweedie*", with thin tapering leaves 2–3 cm. long; and (3) another small plant with leaves sometimes tending to be spathulate, like those of the type, though in one specimen they are thin and grass-like and up to 4 cm. in length; the spathulate-leaved plants have leaves about 2 cm. long.

The plant described as *C. attenuata* by Hook. & Arn. appears to be the large specimen, No. 1 above, which unfortunately has no ripe fruits.

It is marked by having *many-flowered* umbels in contrast to the smaller specimens on this sheet, which have only 4–6 flowers in an umbel.

The specimen from the Rio Primero in Herb. Kew., collected by *Hieronymus* (1878), may also belong to this variety.

The Brazilian specimen (*Rose & Russell*), is doubtfully referred to this species, as it is without flowers or fruit, but the foliage resembles that of this variety.

5. **Lilæopsis Schaffneriana** (*Schlecht.*) *Coulter & Rose* in Bot. Gaz. xxiv. p. 48, fig. 3, 1897; N. Amer. Umbellif. p. 125, fig. 39, partim (specim. ex S. Arizona et Chile excepta).

*Crantzia Schaffneriana* Schlecht. in Linnæa, xxvi. p. 370 (1854); *C. lineata* Hemsley, Biolog. Cent.-Amer. i. p. 569, non Nutt.; *C. lineata* Nutt. *forme isoetoide* Chodat, Bull. Soc. Bot. Genève, 2^me^ sér. xii. p. 29 (1920), partim.

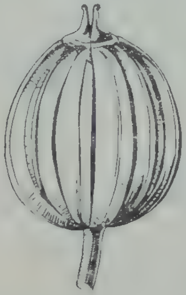
(Descr. emend. et ampl.) *Pedunculi* 1–2 cm. longi, 6–8-flori; pedicelli 5 mm. longi. *Fructus* orbicularis, compressus, 1·75 mm. longus, 1·75–2 mm. latus, costis 5 acutis, sclerenchymate in sectione transversali usque ad superificiem internam pericarpii attingente; vittæ 6, quarum 2 commissurales. (Plate **19**. fig. 2.)

Var. *a*. **subterrestris** Schlecht. in Linnæa, xxvi. p. 371.

Mexico. Near Chapultepec (July 1854), *Schaffner* in Herb. Kew.; San Luis Potosi, Morales, in marshes (August 1877), *Schaffner* No. 1 in Herb. Kew.; *Schaffner* 543 in U.S. Nat. Herb.; San Luis Potosi, 1835–2450 m., *Parry & Palmer* 287 in Herb. Kew., Edin., Gray Herb. et U.S. Nat. Mus.; Puebla, Laguna de San Baltasar, 2135 m., *G. Arsène* 1304 in U.S. Nat. Herb.; Valley of Mexico, *J. N. Rose & J. S. Rose* 11500 in U.S. Nat. Herb.

Ecuador. Rio de Huano; in meadows (Nov. 1858), *R. Spruce* 5751; Rio Chambo, in damp meadows (Jan. 1859), *R. Spruce* 5751 in Herb. Kew., Edin. et Herb. Mus. Paris; Rio de Huano, in damp places (Nov. 1858), *R. Spruce* 5782 in Herb. Kew., Herb. Mus. Paris, Herb. Regnell. Stockh. et Gray Herb.

Text-fig. 5.



*L. Schaffneriana* (Schlecht.) Coulter & Rose. × 15.

Var. *b*. **aquatica** Schlecht. *l. c.*

Mexico. Valley of Mexico; in ditches, *Bourgeau* 643 in Herb. Mus. Paris; Jalisco State, Orindam, *Rose & Hough* 4799 in U.S. Nat. Herb.; near Chapultepec *Rose & Hough* 4545 in U.S. Nat. Herb.

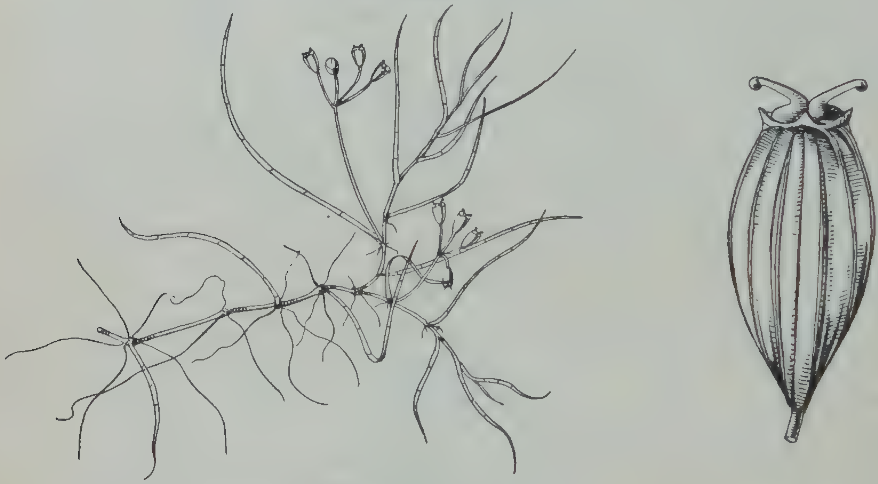
Ecuador. Rio de Huano; in flowing water (Nov. 1858), *R. Spruce* 5783 in Herb. Kew., Edin., Herb. Mus. Paris, Herb. Regnell. Stockh. et Gray Herb.

There is a Colombian specimen at Kew, collected by W. Purdie in December 1845, in moist places on the plain of Bogota, which may be *L. Schaffneriana*. It bears stout upright leaves and simple immature umbels of flowers. The rhizome, however, is stouter than is usually seen in *Lilæopsis*, and the specimen, but for the simple umbels, closely resembles *Ottoa* H. B. & K., which is found in Colombia.

6. **Lilæopsis tenuis** *A. W. Hill.* Species gracillima, fructibus elongatis non-lignosis, distincta.

*Folia* 2–4 cm. longa, 0·5 mm. lata, gracillima. *Pedunculi* circiter 1 cm. longi, 2–3-flori. *Fructus* 2·5–2·75 mm. longus, 1–1·25 mm. latus, costis 5 exiguis tenuibus non-lignosis instructus ; vittæ 6, quarum 2 commissurales.

TEXT-FIG. 6.



*L. tenuis* **A.** W. Hill. ×2.

Fruit. ×15.

BRAZIL. Paraná : Tamandaré ; in marshy places (November 1924), *G. Jönsson* in Herb. Regnell. Stockh.

This is the most delicate and slender of all the species, and closely resembles a freshwater Alga in general appearance. The leaves and fruits are semi-transparent, and the plant evidently lives partly submerged.

7. **Lilæopsis andina** *A. W. Hill.*

*L. attenuata* Fernald in Rhodora, xxvi. p. 94 (1924), quoad specim. andin. tantum.

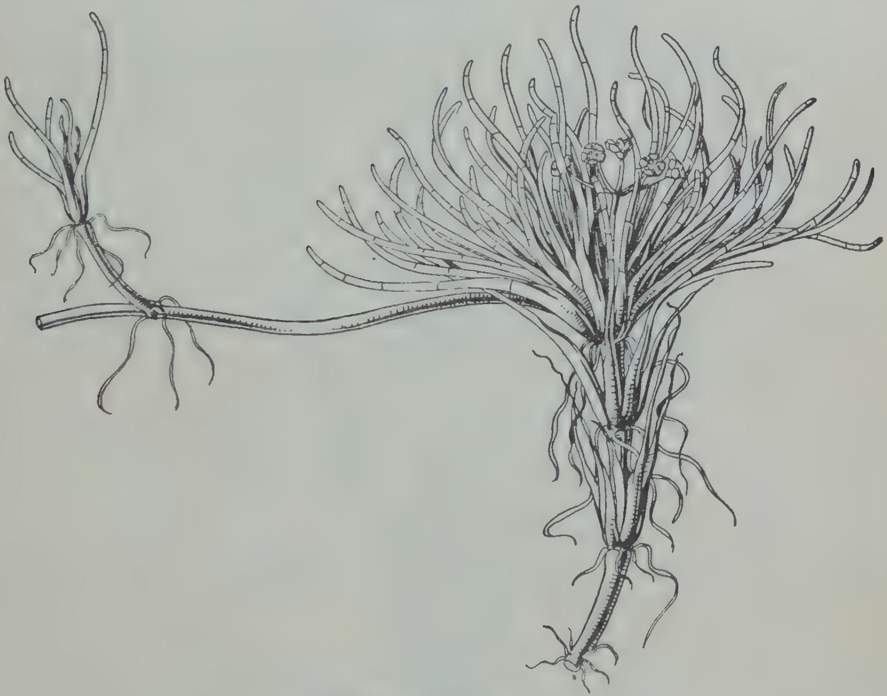
*Crantzia lineata* Gay, Fl. Chil. iii. p. 127 ; Wedd. Chlor. And. ii. p. 201, tab. 68 ; Ann. Univ. Santiago, 1872, p. 725 ; Reiche, Fl. Chil. iii. p. 117, partim.

Species fructibus costis rotundatis *L. maclovianæ* (Gandog.) A. W. Hill, affinis, sed costis lateralibus applanatis et fructibus minoribus distincta.

*Herba* cæspitosa, muscosa ; rhizoma repens elongatum. *Folia* dense conferta, 1·5–2·5 cm. longa, rarius 6 cm. longa, multisepta, linearia. *Pedunculi* 3–6-flori, 4–5 mm. longi ; pedicelli 3–10 mm. longi ; bracteis involucri minutis vel nullis. *Fructus* ovoideus, 1·75 mm. longus, 1·5–1·75 mm. latus, costis rotundatis, lateralibus in sectione transversali conspicuis, e cellulis lignosis compositis; vittæ 6–8, quarum 2 vel 4 commissurales. (Plate **20**. fig. 3.)

Bolivia. Guaqui: Lake Titicaca; 3820 m. *A. W. Hill* 196 in Herb. Kew.; Larecaja Province, near Sorata in mud, River Ucumarini, 3200 m., *Mandon* 575 in Herb. Kew., Mus. Brit., Herb. Mus. Paris, Gray Herb. et Herb. Boiss.; Guaqui, 3820 m., *Buchtien* 5964 in U.S. Nat. Mus. et Herb. Kew.; Dep. La Paz, Prov. Murillo, La Paz, 3900 m., *Asplund* 582; Palca, 3600 m., *Asplund* 823; Challapampa, 3800 m., *Asplund* 610; Prov. Pacajes, near Corocoro, 4200 m., *Asplund* 4478; General Campero, 3900 m., *Asplund* 407; Ulloma, 3800 m. (? var.), *Asplund* 2567; Prov. Ingavi, Comanche, 4100 m., *Asplund* 4479; Viacha, 3850 m., *Asplund* 2164, omnes in Herb. Reg. Stockh. et Mus. Bot. Upsala et Herb. Kew.

Text-fig. 7.



*L. andina* A. W. Hill. × 2.

Argentine. Prov. Jujuy: Moreno; river-bank, 3800 m., *R. E. Fries* 705 *a*, in Herb. Reg. Stockh. et Herb. Kew.

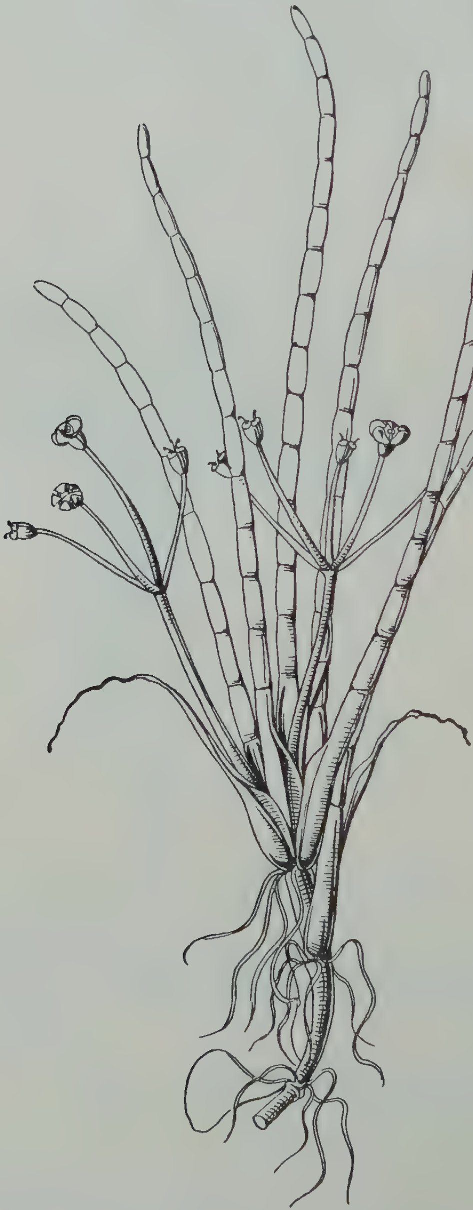
7 *a*. **Var. inundata** (*Mandon*) *A. W. Hill.*

*Folia* usque ad 10 cm. longa, teretia, basi 3 mm. lata. *Fructus* ignotus.

Bolivia. Prov. Omasuyos: near Achacache and Amapusa; in marshes, 3950 m., *Mandon* 976 in Herb. Kew., Herb. Mus. Paris, Herb. Boiss. et Gray Herb.; Prov. Larecaja: near Sorata, 3800–4200 m., *Mandon* 577 in Herb. Mus. Brit.; Dept. La Paz, Prov. Murillo, Palca, Lake

Choquecota, circa 4400 m., *Asplund* 903 in Herb. Regnell. Stockh. et Herb. Kew.; Peru Central, *Weddell* 4411 in Herb. Mus. Paris.

TEXT-FIG. 7 *a*.



*L. andina* A. W. Hill. × 2.

This variety is probably only due to the plant growing partly under water, the leaves in consequence are strongly developed and flowers are few and small.

7 *b*. Var. **multivittata** *A. W. Hill.*

*Fructus* 2 mm. longus, 1–1·25 mm. latus, costis rotundatis, lateralibus in sectione transversali magnis lateraliter extensis; vittæ 10, quarum 6 commissurales. (Plate **20**. fig. 2.)

Argentine. Prov. Mendoza: near Aconcagua; Puente del Inca, *Malme* 2945 in Herb. Regnell. Stockh. et Mus. Bot. Stockh.

Chile. Uspallata Pass: Juncal; in swamps, 2200–3000 m. (14. ii. 1903), *Buchtien* in Herb. Regnell. Stockh., Herb. Edin. et Herb. Mus. Brit.

The fruits of this species show some variation in the number of vittæ. In Asplund's specimens from Bolivia only two vittæ are to be found at the commissure, while Mandon's specimens show either two, three, or four vittæ at the commissure.

The specimens from the Uspallata Pass (*Malme* and *Buchtien*), show six vittæ at the commissure and, as the fruits are also longer and somewhat more elongated along the commissure, with much larger lateral lignified ribs, it has seemed best to describe them as a variety of *L. andina.*

It is of interest to notice that both in the enlargement of the lateral ribs and the multiplication of the vittæ this variety *multivittata* shows similarity in its fruits to those of *L. macloviana* (Gandog.) A. W. Hill.

8. **Lilæopsis sinuata** *A. W. Hill.*

*Lilæopsis attenuata* Fernald in Rhodora, xxvi. p. 94 (1924), quoad specim. Chilens. tantum.

*L. Schaffneriana* Coult. & Rose, Bot. Gaz. xxiv. p. 48, quoad specim. Chilens. Philippianum tantum.

*Crantzia lineata* Gay, Flor. Chil. iii. p. 127; et Reiche, Flor. Chil. iii. p. 117 partim.

Species *L. maclovianæ* (Gandog.) A. W. Hill, affinis, sed foliis gracilibus cæspitosis, fructibus minoribus vittis 6 præcipue differt.

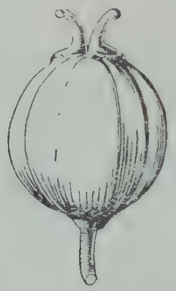
*Herba* dense cæspitosa; rhizoma repens. *Folia* 3–4 cm. longa. *Pedunculi* 2 cm. longi, 4–10-flori. *Fructus* rotundatus, compressus, 1·5–1·75 mm. longus et latus, costis dorsalibus acutis, lateralibus conspicuis expansis, dorsalibus in sectione transversali sclerosis, lateralibus magnis, lignosis; vittæ 6, quarum 2 commissurales. (Plate **20**. fig. 6.)

Chile. Island of Chiloe; Ancud (1861), *Philippi* in Herb. Kew. et Herb. Boiss.; Chiloe, *Werderman* 290 in Herb. Mus. Brit.; Chiloe, Cucao, *Gay* 206 in Herb. Mus. Paris; Corral near Valdivia, *Philippi* 671 in Herb. Kew.; Quillota, *Philippi* in Herb. Boiss.; Valdivia, *Buchtien* in U.S. Nat. Herb. 1134376; Prov. Concepcion, *Philippi* in U.S. Nat. Herb. 55010. Valparaiso, *Bertero* 1046 in Herb. Mus. Paris; Campana de Quilotta, *Germain* in Herb. Mus. Brit. (?).

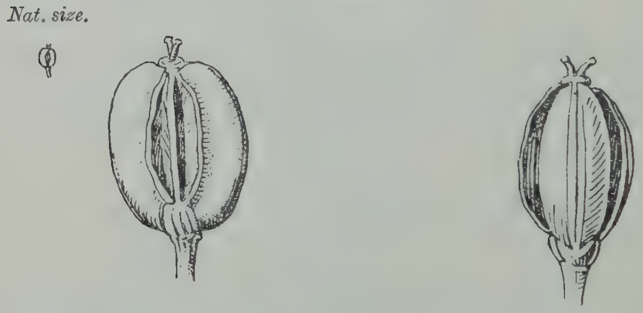
A specimen collected near Mt. Dinero at the eastern end of Magellan Straits by *R. O. Cunningham* (Feb. 1868), both at Kew and at Harvard, may belong to this species, but the specimens are too imperfect for exact determination.

This species shows relationship in its fruit-structure with *L. occidentalis* Coult. & Rose, from western N. America, and also with *L. macloriana* (Gandog.) A. W. Hill, from the Falkland Islands, and with *L. Brownii* A. W. Hill, from Bass Strait, Tasmania.

These all show well-developed laterally-extended lateral ribs to the mericarps, composed of large, pitted, lignified cells. *L. macloviana* is distinguished by its large fruits which show five or six vittæ at the commissure, whilst in *L. Brownii* there may be as many as sixteen vittæ in each mericarp, two or three occurring between each of the ribs.



Text-fig. 8.—*L. sinuata* A. W. Hill. × 15.
(Ancud, *Philippi.*)



Text-fig. 9.—*L. sinuata* (Chiloe, *Werderman* 290). × 10.

*L. sinuata* and *L. occidentalis* possess only two vittæ at the commissure. In the fruit of *L. sinuata*, however, the lateral patches of tissue are much larger and more extended than in *L. occidentalis*, the whole fruit being more compressed, and the dorsal ribs are more prominent.

*L. occidentalis* appears to be a much more strongly developed plant than *L. sinuata* and has longer and stouter leaves.

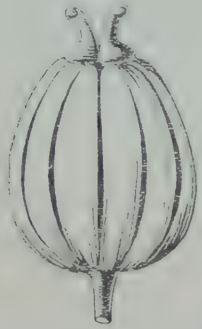
9. **L. macloviana** (*Gandog.*) *A. W. Hill.*

*Crantzia lineata* Hook. f., Fl. Ant. ii. p. 287, Tab. 100 ; Reiche, Fl. Chil. iii. p. 117, partim ; non Nutt.

*Crantzia macloviana* Gandoger in Bull. Soc. Bot. France, lxv. p. 31 (1918), sine descr.

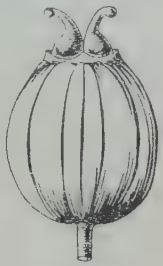
*Rhizoma* repens. *Folia* 2–14 cm. longa, cæspitosa. *Umbella* 4–7-flora, foliis duplo- vel triplo-breviora. *Fructus* 2–2·25 mm. longus, 1·75 mm. latus, obovoideus, compressus, costis rotundatis lateralibus multo majoribus conspicuis, lateralibus in sectione transversali magnis lignosis ; vittæ 8–10, quarum 4–6 commissurales. (Plate **20**. fig. 1.)

TEXT-FIG. 10.



*L. macloviana* (Gandog.) A. W. Hill. × 15.
Hooker.

TEXT-FIG. 11.



*L. macloviana.* × 15.
Skottsberg 101.

FALKLAND ISLANDS. Antarctic Expedition ; 1839–1843, *J. D. Hooker* in Herb. Kew. et Herb. Mus. Paris ; East Falkland, Rabbit Cove, in deep sand (10. ii. 1908), *C. Skottsberg* 101 ; Port Harriet, *Skottsberg* 101 in Mus. Bot. Stockh. et Herb. Upsala ; Port Stanley (30. iii. 1902), *Skottsberg* 96 in Mus. Bot. Stockh. ; West Falkland, Roy Cove Creek, just above tidal marks, *Mrs. Vallentin* 96 in Herb. Mus. Brit. ; Falkland Is., *Miss F. J. Hennis* in Herb. Mus. Brit.

TIERRA DEL FUEGO. Rio Arsopaga, *P. Dusén* 599 in Mus. Bot. Stockh. et Herb. Upsala.

? PATAGONIA. Sta. Cruz Territory : Pescadores ; near Sta. Cruz, *P. Dusén* 5455 in Mus. Bot. Stockh.

? SOUTH GEORGIA. H.M.S. 'Sappho' in Herb. Kew.

It is not certain whether the specimens from Patagonia and from South Georgia are rightly referred to *L. macloviana*. Dusén's no. 5455 has very immature fruits, but the vittæ which may be from 8–10 can be clearly seen. In its general facies the specimens resemble those from the Falkland Islands.

The South Georgia specimens bear neither flowers nor fruits, and are tentatively included under *L. macloviana* on account of their geographical distribution.

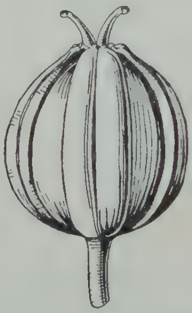
**10. Lilæopsis Brownii** *A. W. Hill.*

*Crantzia lineata* Benth., Flora Australiensis, iii. p. 374, quoad specim. Tasmaniæ; Hooker, Flora of Tasmania, i. p. 160 (quoad *Gunn* sp.).
*Hydrocotyle fistulosa* Brown MS. in Herb. Mus. Brit.

Species *L. maclovianæ* (Gandog.) A. W. Hill, affinis, sed vittis numerosis distincta.

*Herba* cæspitosa. *Folia* gracilia, linearia, attenuata vel paullo spathulata, 3–10 cm. longa vel longiora. *Pedunculi* 1–3 cm. longi, 4–8-flori. *Fructus* late ovoideus, paullo compressus, 1·5–2 mm. longus, 1·5–1·75 mm. latus, costis dorsalibus inconspicuis, lateralibus magnis conspicuis in sectione transversali costis lignosis conspicuis; vittæ 13–16, quarum 2 vel 3 in quaque area intercostali dispositæ, 5–6 commissurales. (Plate **20**. fig. 5.)

TEXT-FIG. 12.



*L. Brownii* A. W. Hill.
R. Brown.

TASMANIA. On inundated banks of rivers in larger islands of Kent's Group (Dec. 12–19, 1803); Bass Strait, *R. Brown* no. 17, in Herb. Mus. Brit. (4552 in Herb. Kew. et Edin., Herb. Mus. Brit. Distrib.) et in Herb. Mus. Paris; Arthur's Lakes and Marshes near Launceston (18. xii. 1845; 17. i. 1845; 23. xii. 1844; 24. xii. 1844), *Gunn* 2008 in Herb. Kew. et Herb. Mus. Paris. (?) Tasmania. *Hooker fil.* in Bot. Mus. Upsala; (?) Strahan, tidal edge of shore, *L. S. Gibbs* 6870; (?) Central Plateau, Lake Elizabeth by Great Lake, creeping on sand or mud, 1000 m., *L. S. Gibbs* 6782.

The two specimens collected by L. S. Gibbs, unfortunately, are without fruits or flowers, so that their exact identity is somewhat uncertain.

This species with its laterally compressed fruits, showing large lateral corky patches, is allied to *L. macloviana* (Gandog.) A. W. Hill, from the

Falkland Islands. It differs principally in its most cæspitose vegetative habit and in the large number of oil-vittæ in the fruit. There may be as many as three vittæ between each of the dorsal ribs instead of one, which is the usual number in all other species, and five or six vittæ are to be found at the commissure. (Plate **20**. fig. 5.)

*L. Brownii* appears to be confined to Tasmania and the Islands of Bass Strait, and has not been recorded from Australia. This and Caley's specimen from Paramatta have both been given the MS. name of *Hydrocotyle fistulosa*, in the one case by Caley and in the other by Robert Brown. The name *fistulosa*, being more appropriate for Caley's larger plant, has been retained for that species, and the Tasmanian plant has been named in memory of R. Brown, who collected it in 1803.

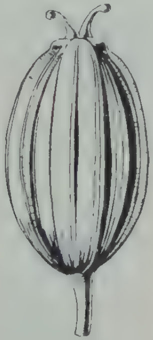
11. **Lilæopsis australica** (*F. Muell.*) *A. W. Hill.*

*Crantzia australica* F. Muell., First Report, p. 13 (1853); Linnæa, xxix. p. 714, non *C. lineata* Nutt.

*C. lineata* Bentham, Flora Australiensis, iii. p. 374, quoad specim. e Terr. Victoria et S. Australia.

*C. polyantha* Gandog. in Bull. Soc. Bot. France, lxv. (1918), p. 31.

TEXT-FIG. 13.



*L. australica* (F. Muell.) A. W. Hill.

*Folia* 6–15 cm. longa, gracilia. *Umbella* 2–6-flora; pedunculi 1–1·5 cm. longi, pedicellis circiter 5 mm. longis. *Fructus* 2·5–3 mm. longus, circiter 1·5 mm. latus, elliptico-ovoideus, costis acutis conspicuis instructus, costis in sectione transversali 5 acutis cellulis sclerosis compositis, lateralibus lignosis; vittæ 8–9, quarum 4–5 commissurales. (Plate **19**. fig. 7.)

AUSTRALIA. Victoria; Yarra River, *F. von Mueller* in Herb. Kew. et Herb. Boiss.; Cudnaka, *F. von Mueller* in Herb. Mus. Paris; Mouth of the Snowy River (E. Victoria), *F. von Mueller* in Herb. Kew.; Port Phillip, *F. von Mueller* in Herb. Mus. Paris; River Barwon, near Geelong, *Oldfield* in Herb. Kew.; Melbourne, *Guilfoyle* in Herb. Edin.; Walcha District, *E. Betche* (12–98) in Herb. Gandog. et Herb. Bot. Gard. Sydney.

South Australia. Kangaroo Island; Cygnet River, *R. Tate* (Dec. 1881); and Mannum, Murray River, *R. Tate* (March 1883) in Herb. Tate (Univ. Adelaide, S. Aust.) et in Herb. Kew.; Kangaroo Island, Harriet River, *T. G. B. Osborn* (24. xi. 1923) in Herb. Kew.; St. Vincent's Gulf, *F. von Mueller* (Fl. Austral.).

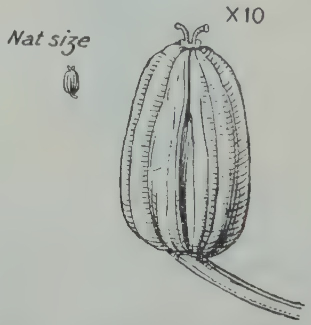
There are some small specimens collected by Mrs. A. Dietrich "near Brisbane River" in 1863–1865, preserved at Kew and at the British Museum, which are referred to this species in the 'Flora Australiensis'; they are, however, more slender and delicate than the specimens described. As they have no mature fruits I hesitate to include them in this species. The South Australian specimens which I have been able to examine through the kindness of Prof. T. G. B. Osborn have ripe fruits, which agree exactly with those of other specimens referred to this species. They are of particular interest, as they confirm the reference in the 'Flora Australiensis' to specimens collected by Mueller in St. Vincent's Gulf, S. Australia.

12. **Lilæopsis fistulosa** (*Caley* MS.) *A. W. Hill.*

*Hydrocotyle fistulosa* Caley MS. in Herb. Mus. Brit.

Species foliis maximis fructibus magnis elongatis conspicue costatis distincta.

Text-fig. 14.



*L. fistulosa* (Caley MS.) A. W. Hill.
G. Caley.

*Rhizoma* repens. *Folia* circiter 30 cm. longa, 5–5·5 mm. lata, multiseptata, leviter moniliformia. *Umbella* 9–10-flora; pedunculi 6–10 cm. longi. *Fructus* 3 mm. longus, 1·75–2 mm. latus, costis 5 acutis conspicuis instructus, costis in sectione transversali triangularibus e cellulis multis minutis lignosis compositis; vittæ 6, quarum 2 commissurales. (Plate **19.** figs. 3, 4.)

Australia. New South Wales; Parramatta, *G. Caley* (Jan. 8, 1804) in Herb. Mus. Brit.

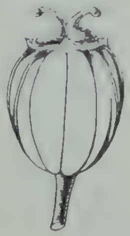
This very striking specimen bears the name *Hydrocotyle fistulosa* in Caley's handwriting in the British Museum Herbarium, and there is a description under this name drawn up by Brown in his MS. There is also a description of Brown's own plant, No. 17, from Bass Strait under the name of *Hydrocotyle fistulosa*, and the specimens at the Museum bear a label with this name in Brown's handwriting. The two plants, however, are quite different both in size and in fruit-structure, Brown's plant showing affinity to *L. macloviana* from the Falkland Islands, while Caley's plant has a fruit so unlike any other species of *Lilæopsis* that it is open to doubt whether it is rightly included in the genus.

It is very unfortunate that Caley's plant does not occur, as far as is known, in any other Herbarium. A careful study of living plants, could they be found, might result in some light being thrown on the relationships of the species.

The fruits differ from those of all other species of *Lilæopsis* in having the five triangular ribs composed of very small lignified cells with small sclerenchymatous patches at the tips or angles of the ribs as seen in transverse section; there is also a pad of this small-celled tissue in the middle of each mericarp between the two commissural vittæ. The two patches of large-celled lignified tissue on either side of this central pad of small-celled tissue are similar to the patches of lignified cells seen especially in the two large lateral ribs of the fruits of other species. (Plate **19**. figs. 3 & 4.)

A specimen, leaves only, collected by Mueller at Lake Calvert, preserved at Paris, should possibly be referred to this species.

TEXT-FIG. 15.



*L. novæ-zelandiæ* (Gandog.) A. W. Hill.

Bidwill 94.

13. **Lilæopsis novæ-zelandiæ** (*Gandog.*) *A. W. Hill.*

*Crantzia lineata* J. D. Hooker, Flora New Zealand, i. p. 87; Handbook New Zealand Flora, p. 89; Kirk, Student's Flora, p. 199; Cheeseman, New Zealand Flora, p. 207, partim, non Nutt.

*C. Novæ-Zelandiæ* Gandog. in Bull. Soc. Bot. France, lxv. (1918), p. 31.

Species fructibus ovoideis, costis subacutis lateralibus majoribus vittis 8 distincta.

*Herba* cæspitosa; rhizoma repens. *Folia* 3–12 cm. longa, attenuata. *Umbella* tenuis, 3–4-flora, bracteis involucri 2–2·5 mm. longis; pedunculi 1–2 cm. longi, pedicellis 5–7 mm. longis. *Fructus* ovoideus, 1·25 mm. longus, 1·5–1·75 mm. latus, costis distinctis subacutis lateralibus majoribus, lateralibus in sectione transversali conspicuis lignosis; vittæ 8, quarum 4 commissurales. (Plate **20**. fig. 7.)

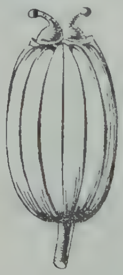
NEW ZEALAND, South Island; Bluff Harbour, *Kirk* 329 in Herb. Mus. Brit.; Nelson, *Bidwill* 94 in Herb. Kew.; *Colenso* 19 in Herb. Kew.; near Dunedin, Tomahawk Lagoon (1896), *G. M. Thomson* in Herb. Gandog. New Zealand, *Sinclair* ex herb. Hooker; and "New Zealand Coll. donné par Sir W. Hooker" in Herb. Mus. Paris; Waikouwaitai Lagoon, Otago, *D. Petrie* (1889) in Gray Herb.?

Gandoger's specimen is only a small scrap with imperfect inflorescences bearing remains of three flowers, and it is on this character alone that he made the Thomson plant a new species.

From the more ample material at Kew and at the British Museum, four-flowered umbels are found to be typical. The fruits, however, afford the only useful characters for specific determination.

In the Paris Herbarium there are two specimens of this species, presented by Sir W. Hooker, which are not represented at Kew.

TEXT-FIG. 16.



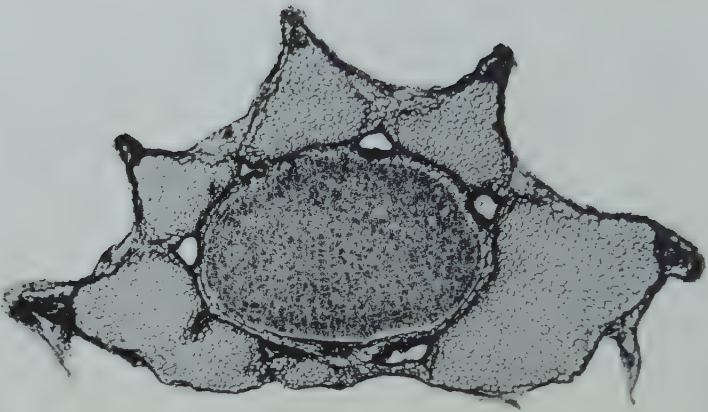
*L. lacustris* A. W. Hill.

### 14. Lilæopsis lacustris *A. W. Hill.*

*Crantzia lineata* J. D. Hooker, Flora New Zealand, i. p. 87; Handbook New Zealand Flora, p. 89; Kirk, Student's Flora, p. 199; Cheeseman, New Zealand Flora, p. 207 partim, non Nutt.

Species fructibus cylindricis, costis rotundatis, vittis 6 distincta.

*Rhizoma* repens. *Folia* 8–15 cm. longa, filiformia, septis distantibus. *Umbella* 5–7-flora; pedunculi 2–3 cm. longi, pedicellis 1–1·5 cm. longis. *Fructus* cylindricus, 2 mm. longus, 1 mm. latus, costis rotundatis; vittæ 6, quarum 2 commissurales.



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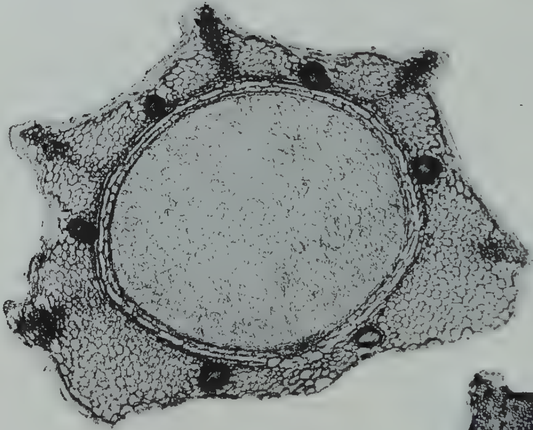

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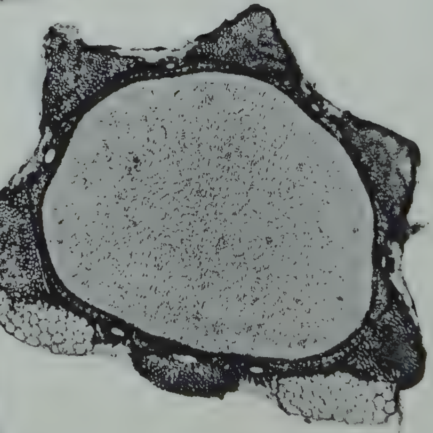

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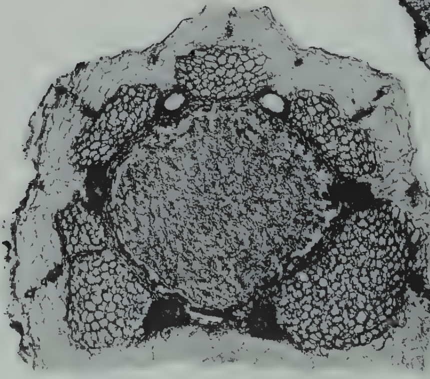

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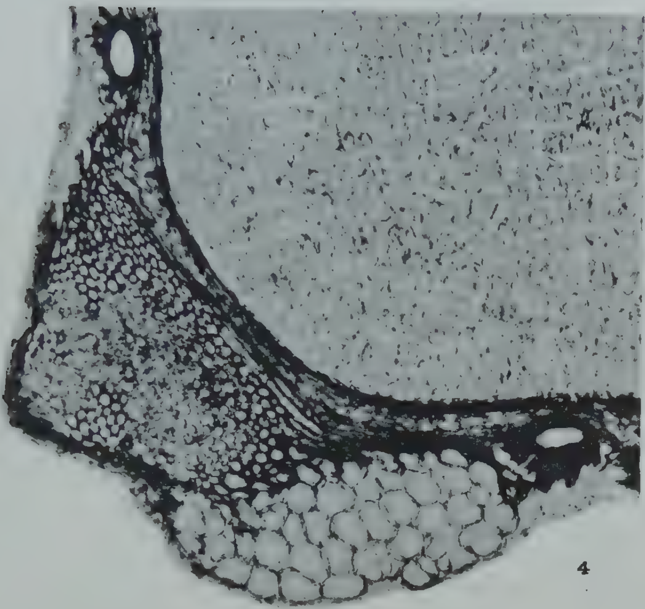
LILAEOPSIS, GREENE.



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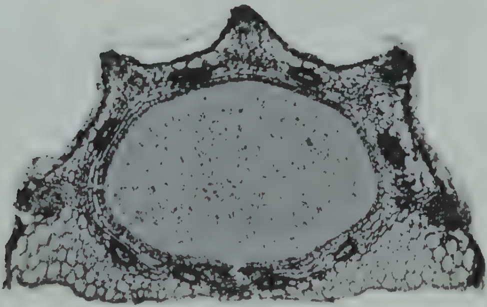

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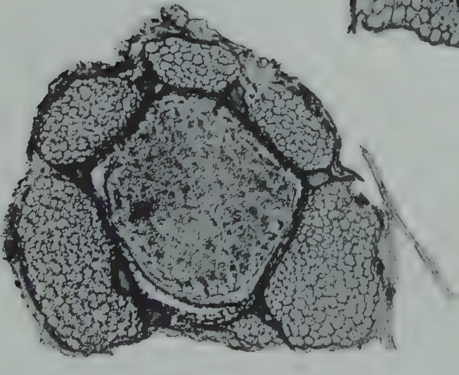

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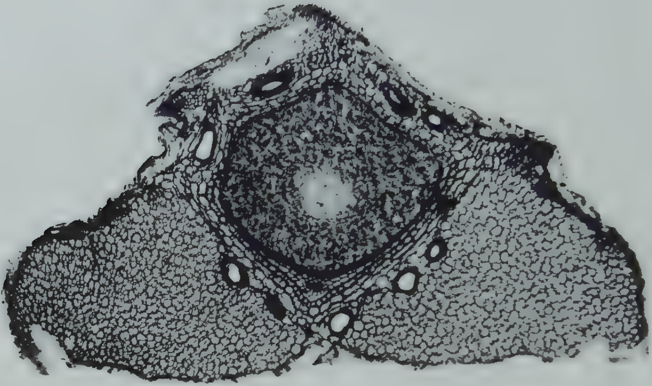

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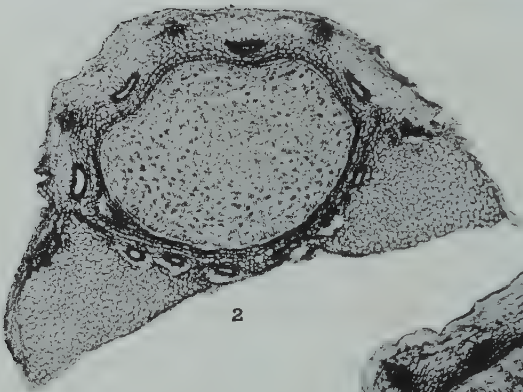

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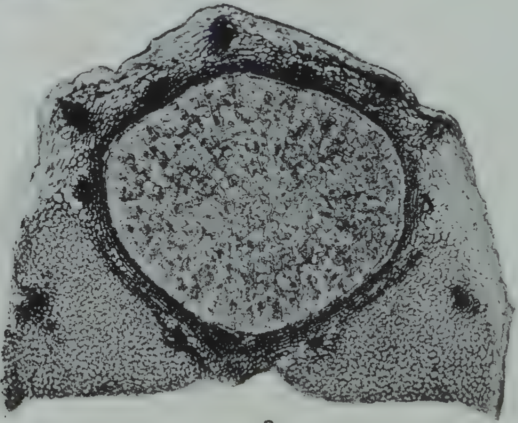

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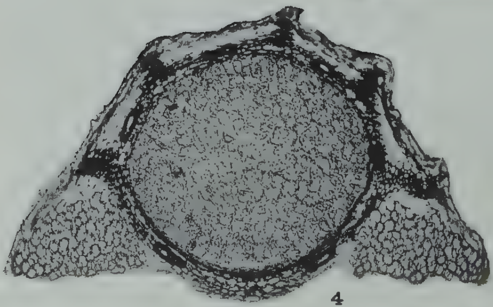

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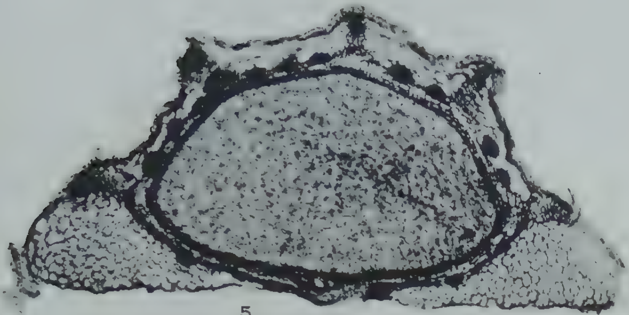
LILAEOPSIS, GREENE.



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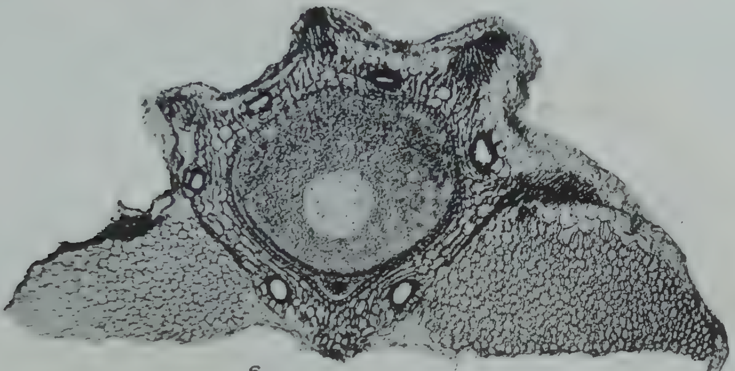

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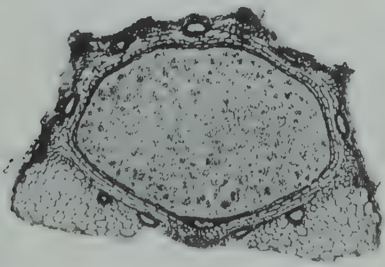

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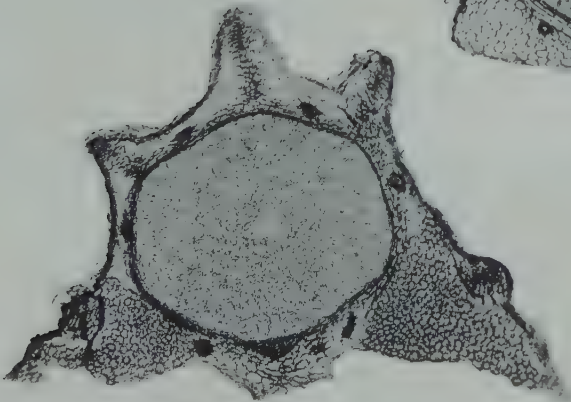

8

LILAEOPSIS, GREENE.

NEW ZEALAND. North Island; Lake Rotorua, *Berggren* in Mus. Bot. Stockh., Upsala et Herb. Boiss.; Lake Rotokakahi, lacustrine form, *T. Kirk* 500 in Herb. Kew.; Wellington, *Dr. Hector* in Gray Herb.; Thames River, *Cheeseman* in U.S. Nat. Herb.; Auckland (Dec. 1878), *Cheeseman* in Herb. Edin. (?).

The specimen collected by *T. Kirk*, no. 500 in Herb. Kew., lacustrine form from Rotokakahi (N. Island), "sometimes found in water 12 feet deep but never producing flowers," may belong to this species, though the "leaves" on the Kew sheet are somewhat stouter than those of the Berggren specimens.

The Kirk specimen is of particular interest, since, as already explained, it affords the true explanation of the morphological character of the "leaves" of this genus (see text-fig. 1, p. 528).

## EXPLANATION OF THE PLATES.

The sections of the fruits were cut by Mr. L. A. Boodle, Assistant Keeper of the Jodrell Laboratory, and the microphotographs reproduced in the Plates were taken by Dr. G. H. Rodman of Putney. I am greatly indebted to both these gentlemen for their very kind and valuable help. Some of the Text-figures were drawn by Mr. G. Atkinson and some by Mr. Trevithick.

### PLATE 19.

All except fig. 4 × 55.

Fig. 1. *L. carolinensis* Coult. & Rose.  
2. *L. Schaffneriana* (Schlecht.) Coult. & Rose.  
3. *L. fistulosa* A. W. Hill.  
4. ,, ,, one of the ribs enlarged × 10.  
5. *L. recurva* A. W. Hill. Young fruit, outer cells filled with starch.  
6. ,, ,, showing the five similar rounded ribs.  
7. *L. australica* A. W. Hill.

### PLATE 20.

All × 55.

Fig. 1. *L. macloviana* (Gandog.) A. W. Hill.  
2. *L. andina* A. W. Hill var. *multivittata* A. W. Hill.  
3. *L. andina* A. W. Hill.  
4. *L. occidentalis* Coult. & Rose.  
5. *L. Brownii* A. W. Hill.  
6. *L. sinuata* A. W. Hill.  
7. *L. novæ-zelandiæ* (Gandog.) A. W. Hill.  
8. *L. chinensis* (L.) Kuntze.

# The Vascular Supply of the Bracts of some Species of *Anemone*[*]. By A. EVELYN CHESTERS, M.Sc., University College, Nottingham. (Communicated by H. S. HOLDEN, D.Sc., F.L.S.)

(PLATES **21–36**, and 9 Text-figures.)

[Read 18th November, 1926.]

## INTRODUCTION.

THE Ranunculaceæ, being held by the majority of modern systematists to form a relatively primitive order, have been regarded as a group from which some suggestion as to the origin of perianth in flowers might be obtained. In this problem four types of "leaf" come under consideration: (*a*) the so-called "honey leaves"—"leaf-structures of the flower, the essential function of which lies in honey secretion" (**6**); (*b*) corolla; (*c*) calyx; (*d*) bracts. The derivation of honey leaves from stamens by a process of sterilisation appears to be a generally accepted fact, but there is a difference of opinion as to what structures should be included under the term "honey leaves." Many botanists restrict this term to the small staminodal structures of certain species of *Clematis* and the more typical honey leaves such as are present in *Eranthis*, while Prantl (**6**) also includes the large petaloid leaves of *Aquilegia* and species of *Ranunculus* which are usually termed corolla.

Concerning the origin of calyx and corolla, there are two principal hypotheses to be noted. Worsdell (**11**), on the one hand, considers that "honey leaves" are a transitional stage in the modification of stamens to form petals—these, again, by further modification, giving rise to sepals. Worsdell, indeed, derives not only corolla and calyx but also bracts and foliage leaves from sporophylls by this process of sterilisation, thus pushing the "sterilisation theory" of sporophytic elaboration outlined by Bower (**2**) to its extreme limit.

Prantl (**6**), on the other hand, draws a sharp distinction between honey leaves and true perianth leaves, and regards the perianth in the Ranunculaceæ as being of foliar nature, preferring the terms "bracteoid" and "petaloid" perianth leaves to "calyx" and "corolla." This derivation of perianth leaves from bracts is upheld by Salisbury (**9**) as the result of a statistical study of members of the Ranunculaceæ. On this view, therefore, a part of the perianth at least is regarded as produced by the modification of foliage leaves, involucral bracts being a transitional stage in this process.

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[*] Thesis accepted for the degree of M.Sc. in the University of Liverpool.

In this connection the genus *Anemone* is of particular interest, since it possesses a very characteristic involucre of three bracts surrounding the flower stalk, and shows marked variations in both position and form of the involucre in different species. In some, notably *A. Hepatica,* the involucre in form and function closely approaches a typical calyx such as is found in *Ranunculus Ficaria*, whilst in others (*A. nemorosa*, for example) it is distinguishable from the foliage leaves only by its position.

Existing views on the relationship of the involucre of *Anemone* and the calyx of *Ranunculus Ficaria* appear to have been founded on a morphological study of the peduncle and bracts of the numerous species of *Anemone* and of the calyx of *R. Ficaria*, anatomical investigation being almost entirely confined to the rhizome and petiole of *Anemone.* It is possible, however, that an investigation of the vascular supply of the peduncle and bracts of various species of *Anemone*, and of the calyx of *R. Ficaria*, might throw some light on the question of the relationship of these structures, and the present investigation, although of a preliminary nature, has yielded interesting and suggestive results in this connection.

While attention has been specially focussed on the genus *Anemone*, *Ranunculus Ficaria* and *Eranthis hyemalis* have also been studied for purposes of comparison. The species of *Anemone* selected for this investigation—namely, *A. angulosa*, *A. apennina*, *A. blanda*, *A. coronaria*, *A. fulgens*, *A. Hepatica*, *A. japonica*, *A. nemorosa*, *A. Pulsatilla*, *A. palmata*, *A. ranunculoides*, *A. rivularis*, and *A. sylvestris*—are fairly representative of the various types of bract or "hypsophyll" occurring within the genus, and as far as possible normal specimens have been studied.

On morphological grounds these species form a series which would appear to illustrate the transformation of the leafy bracts into a typical calyx-like structure, or *vice versâ*, a transformation marked by distinct anatomical variation. Before proceeding to the detailed anatomical study, it may be helpful to take a brief morphological survey of the types of involucre occurring in the various species, and to note the kind of foliage leaf which accompanies the different types of hypsophyll.

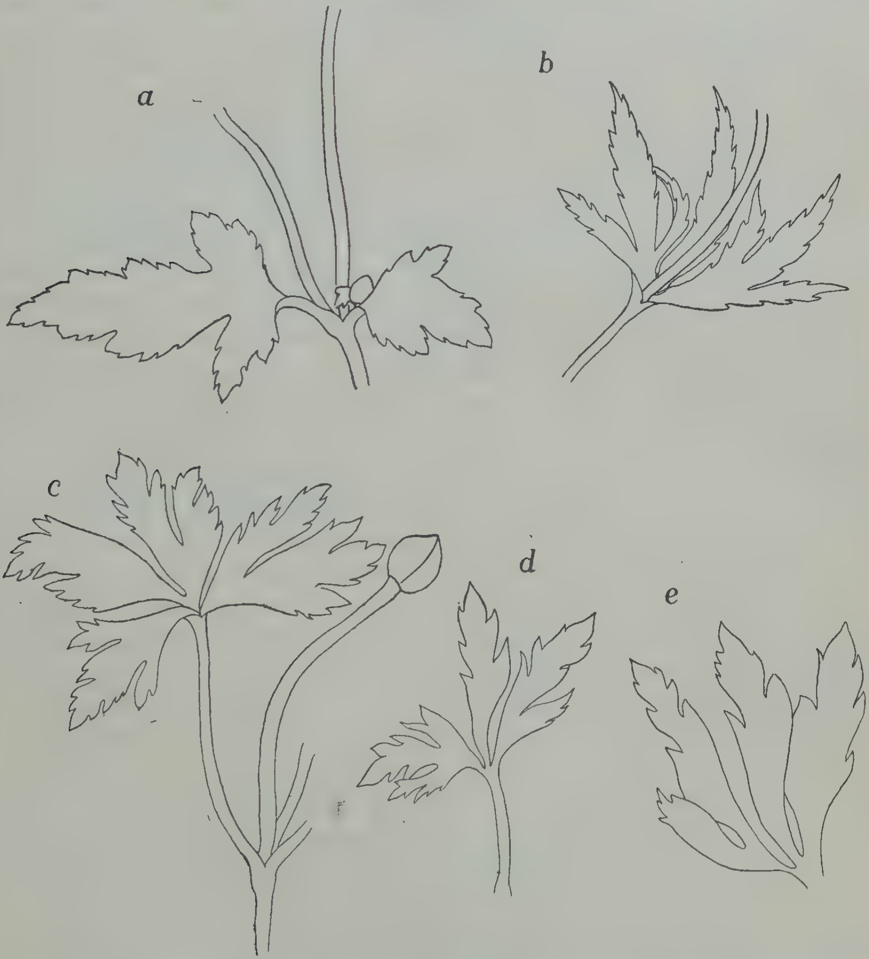
## Position and Form of Bracts.

*A. japonica* may be regarded as representing one end of the series. The flower axis is erect and branches freely, resulting in the cymose inflorescence which is characteristic of the Order. There is no well-marked involucre of three bracts, but at each node usually two hypsophylls arise, each bearing a shoot in its axil. The vegetative leaf consists of a well-developed petiole bearing three short-stalked leaflets. Each leaflet exhibits three main lobes, while the margin is sharply indented. The hypsophylls differ from the foliage leaves in the absence of petiole, and, as they are carried well up into the light by the axis, are capable of functioning as photosynthetic organs (text-fig. 1, *a*).

*A. rivularis* is of the same cymose type, but smaller, and the branching is much more restricted. Both vegetative leaves and hypsophylls are deeply indented. As in *A. japonica*, the hypsophylls—of which, however, there are usually three at each node—are distinguished from vegetative leaves by the absence of petiole (text-fig. 1, *b*).

*A. sylvestris.* The vegetative leaves and hypsophylls consist of a well-developed petiole bearing three sessile leaflets which are slightly segmented.

TEXT-FIG. 1.



*a*, bract of *A. japonica*; *b*, of *A. rivularis*; *c*, of *A. sylvestris*; *d*, bract of *A. nemorosa*; *e*, of *A. ranunculoides*.

The peduncle bears an involucre of three (rarely four) hypsophylls very similar to the foliage leaves. Axillary shoots are characteristic, and show varying degrees of development from insignificant buds to an axis bearing involucre and flower. The presence of the three-leafed involucre is a constant feature of the remaining species (text-fig. 1, *c*).

*A. nemorosa*, *A. apennina, A. blanda.* These species have much in common. In each the vegetative leaf consists of three stalked leaflets and a well-developed petiole. Each leaflet is divided into three lobes which are deeply segmented. The flower axis is unbranched and bears an involucre of three hypsophylls. These are large and leafy, and are only distinguishable from the vegetative leaves by position. The internode between involucre and flower becomes elongated and the involucral leaves function as photosynthetic organs. Although in each species the flower is solitary, in every specimen of *A. apennina* examined a small axillary shoot was present, this becoming evident only in the transverse sections of this region of the plant (text-fig. 1, *d*).

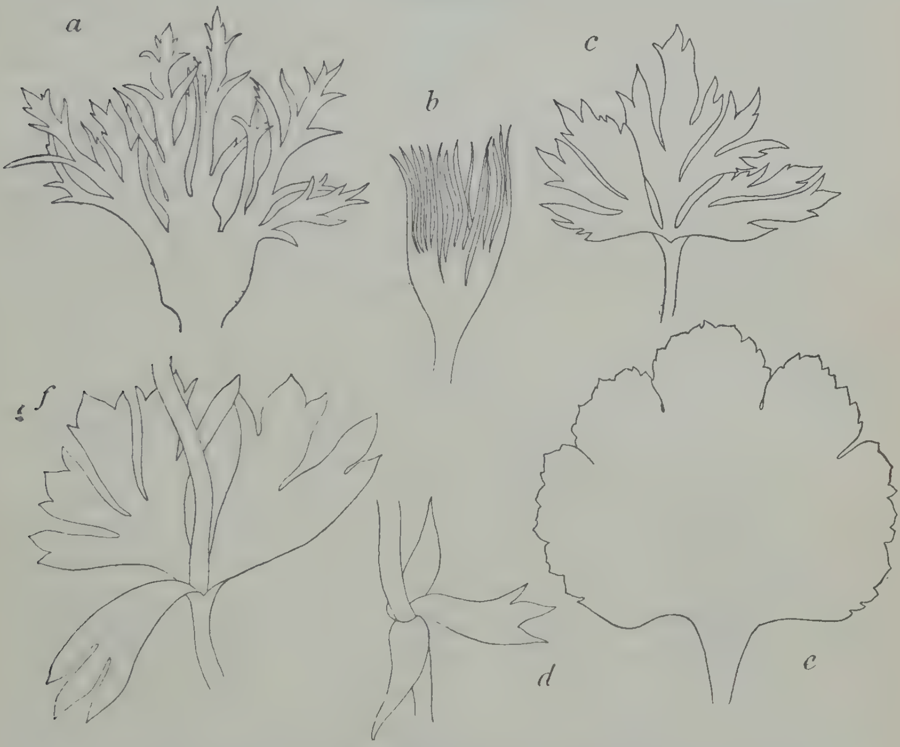
*A. ranunculoides.* The inflorescence is typically solitary, but specimens in which two flowers arise from the involucre are not uncommon, and well-developed axillary shoots are of frequent occurrence. Both vegetative leaves and hypsophylls are of the same type as *A. nemorosa,* but there is a decided reduction in the length of the hypsophyll petioles, accompanied by a broadening of the leaf-base (text-fig. 1, *e*). In one of the specimens examined the axis exhibited the usual three-leafed involucre, but the axillary shoots were particularly well developed, one producing two leaves and a flower, the other two small leaves. It is interesting to note that in species of *Anemone*, where the inflorescence is typically solitary, if axillary shoots are present, two (and not three) leaves are usually produced, even when, as in this case, a flower also arises. It may be noted that in *A. sylvestris,* where the inflorescence is cymose more frequently than solitary, the axillary flower bearing shoots exhibit the usual three-leaved involucre.

*A. coronaria.* The foliage leaf has a petiole several inches long and the lamina consists of three much divided leaflets. The flower arises from an involucre of three bracts, and, though the inflorescence is solitary, two axillary shoots may occur. Frequently one or two additional bracts arise within the typical involucre. The bracts are sessile, with a very broad leaf-base. The lamina is segmented, but to a less extent than the foliage leaves. In its early stages the sheathing bracts closely surround the flower-bud. Later the internode elongates about an inch or an inch and a half, and the involucral leaves take up a horizontal position. The hypsophyll here is thus quite distinct in appearance from the vegetative leaf, the difference lying in the greater development of the leaf-base and a reduction of petiole and lamina—*i. e.*, the adequacy of the hypsophyll as a protective sheathing organ is developing at the expense of its photosynthetic capacity (text-fig. 2, *a*).

*A. Pulsatilla.* The vegetative leaves are of the usual divided type. The involucre closely envelops the flower-stalk. Each bract consists of a broad base and a lamina of three lobes, which are divided into a number of finger-like segments. The bases of the bracts unite and form for a short distance a coherent sheath round the axis. The flower is solitary and no axillary shoots have been observed. The bracts form a more effective sheath for a longer period than in any of the species commented on above, and even when fully developed the internode between involucre and flower elongates to a less extent than in *A. coronaria* (text-fig. 2, *b*).

*A. fulgens* shows a distinct advance in the series. The vegetative leaves resemble those of *A. nemorosa*, but the segmentation is not so pronounced and the petioles of the leaflets are shorter (text-fig. 2, *c*). The involucral leaves are sessile, and the internode between involucre and flower becomes elongated. The bracts are of a much simpler type than any so far considered.

TEXT-FIG. 2.



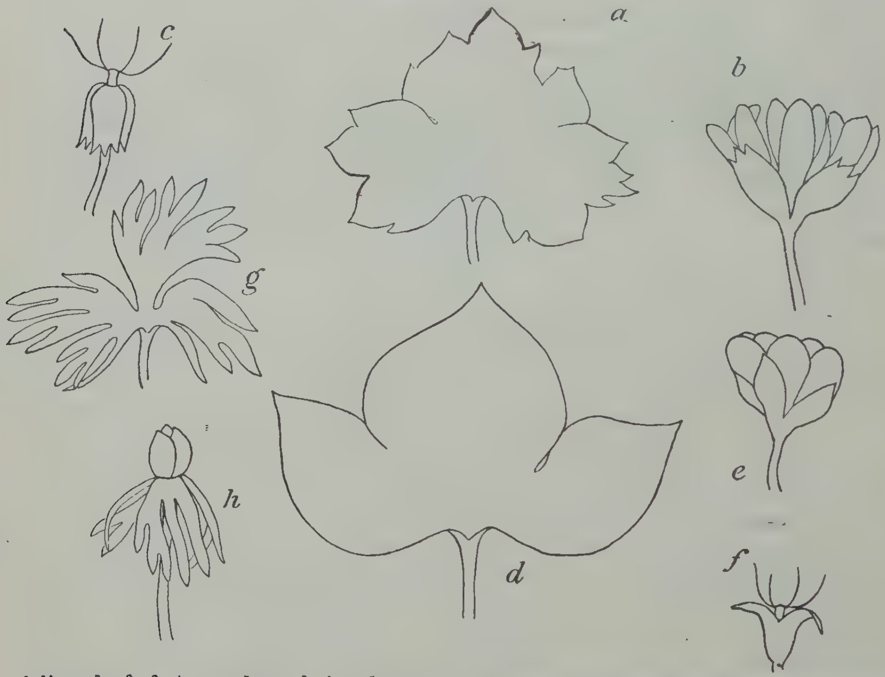
*a*, bract of *A. coronaria*; *b*, of *A. Pulsatilla*; *c*, foliage leaf of *A. fulgens*; *d*, involucre of *A. fulgens*; *e*, foliage leaf of *A. palmata*; *f*, involucre of *A. palmata*.

Of the three, one can be distinguished as the bract, since it is larger and the broad base bears a small lamina of three entire pointed segments. The two bracteoles are typically unsegmented, although occasionally one or both may exhibit slight segmentation. Thus in *A. fulgens* the hypsophylls are of little use as photosynthetic organs, their chief function being that of protecting the flower-bud; hence the reduction of lamina, absence of petiole, and development of base (text-fig. 2, *d*).

*A. palmata* is an exceptionally interesting type. The vegetative leaf has a simple trilobed lamina with a slightly indented margin (text-fig. 2, *e*). The involucral leaves are sessile with broad leaf-bases, and exhibit a much more distinct segmentation than do the vegetative leaves. This segmentation, moreover, is not of the same type as that of the vegetative leaves, but recalls that of species such as *A. coronaria*—a fact noted by Salisbury (**9**). Well-developed axillary shoots are usually present, consisting of two hypsophylls and a flower (text-fig. 2, *f*).

*A. angulosa* is also characterised by a simple vegetative leaf of three lobes with a slightly indented margin (text-fig. 3, *a*). The solitary flower arises from an involucre of three bracts, but as the internode remains very short, the bracts appear to form a calyx. The bracts have broad leaf-bases, which at their proximal end completely surround the flower-stalk. Each is indented at its apex, the indentations forming three pointed teeth, recalling the bract of *A. fulgens* rather than the lobing of the vegetative leaf (text-fig. 3, *b* and *c*).

TEXT-FIG. 3.



*a*, foliage leaf of *A. angulosa*; *b*, involucre of *A. angulosa*; *c*, showing internode between involucre and flower of *A. angulosa*; *d*, foliage leaf of *A. Hepatica*; *e* and *f*, involucre of *A. Hepatica*; *g*, foliage leaf of *Eranthis hyemalis*; *h*, involucre of *Eranthis hyemalis*.

*A. Hepatica* differs from *A. angulosa* in that the margin of the trilobed leaf is entire, and the bracts, which, as in *A. angulosa*, are situated only just below the flower, show no trace of segmentation (text-fig. 3, *d*, *e*, *f*).

In these species of *Anemone* the bracts or hypsophylls show variations along two distinct lines :—

1. In the position of the hypsophylls.

2. In the proportional development of lamina, petiole, and base, a gradual reduction of petiole and lamina accompanying a broadening of the leaf-base.

It is noteworthy that those species in which the hypsophylls show the greatest departure from the segmented leafy type are characterised by a simple vegetative leaf.

Comparing *Ranunculus Ficaria* with the various species of *Anemone*, the vegetative leaf is simple and devoid of any suggestion of lobing or of segmentation. The flower is solitary, and is surrounded by a calyx resembling in appearance the involucre of *A. Hepatica*. Here, however, the "calyx" lies immediately below the "corolla," no internode between the two whorls being evident.

*Eranthis hyemalis.* The vegetative leaf consists of three sessile segmented leaflets. The involucre of three bracts is large and leafy, the bracts resembling the vegetative leaves in size and form. There is, however, no internode between involucre and flower, so that here the leafy bract typical of so many species of *Anemone* is combined with the calyx-like position found in *Ranunculus Ficaria* (text-fig. 3, *g*, *h*).

## THE VASCULAR SUPPLY OF THE BRACTS.

The vascular system of *A. japonica* is greatly complicated by the repeated branching of the flower axis. It seemed better, therefore, to consider first of all a form such as *A. nemorosa*, in which the involucre appears to be constant in the number and position of the bracts and in the absence of axillary shoots.

*A. nemorosa.* In the petiole of each of the three bracts there were five vascular bundles—one midrib, two laterals, and two marginals. As the petiole approached the axis, the laterals divided, one half fusing with the midrib, the other half with the marginal. Occasionally the lateral remained undivided, the whole bundle passing over to the midrib, which at this stage had, owing to the fusion, a very characteristic trilobed appearance.

The petioles meanwhile joined together, thus for a very short distance completely surrounding the stem. The two marginal bundles of each diverged widely from the midrib, so that they approached those of the adjacent bracts and eventually fused with them. Fusion of bundles, both of marginals and of midribs and laterals, was usually completed at this stage before entrance into the main axis, but was occasionally delayed (Pl. **21**, *a*).

Slight variations were observed, such as the presence of small accessory marginal bundles which linked up with the main bundles. Again, the marginals occasionally divided, the inner strand receiving the outer strand of the divided lateral, but eventually fusion with adjacent marginals was achieved and, as before, a ring of six large bundles was formed.

The vascular tissue of the peduncle above the bract node consisted of a single ring of bundles, the number varying between eleven and sixteen, with a general tendency for an alteration of large and small bundles. At the node the bundles became rearranged, resulting in the formation of six gaps in the ring, one being opposite each incoming bundle. Frequently, the small bundles divided first, the two halves diverging and, in some cases, joining the nearest large bundle. The large bundles either divided or merely swung to one side, leaving a gap for the bract bundle. There were now six groups of stem bundles, but fusion between them at this stage was rare.

The usual course taken by the six incoming bundles was as follows :—The three midribs passed into the ring and continued down the peduncle as main bundles. Two of the marginals did likewise, while the third passed to one side and joined a midrib, carrying with it the intervening stem bundles (Pl. **21**, *b*). Occasionally one of the midribs swung across to join a marginal, in which case all three marginals passed down as main bundles. During this process a small strand from an incoming bundle was in some cases given off to join a stem bundle.

Meanwhile, the bundles of each of the six groups approached each other more closely, and a certain amount of division and fusion took place ; a small strand consisting of two or three xylem elements was occasionally cut off from one of the group bundles, and passed a little way into the pith. This small strand persisted for a short time, but eventually passed out again into the ring slightly to one side of its original position and joined the group bundle.

The group bundles now separated into two, or sometimes three, rather irregular masses. These began to turn outwards, approaching each other so closely at first that occasionally it became impossible to define the limits of each. From this point, as the bundles diverged, a single "contact strand" frequently proceeded as a small independent bundle and continued down the stem. Presumably it was formed of elements derived from each of the diverging bundles. Each of these joined the nearest incoming bundle. Fusion between stem and bract bundles was not always completed, in which case the stem bundles formed a subsidiary strand of the peduncle.

Thus the vascular ring of the peduncle below the node consisted of five main bundles, each of these later on passing out into the bracts, and of a number of smaller bundles in groups of one, two, or three, alternating with the main strands. These small bundles might arise (*a*) as contact strands, (*b*) as strands given off from the main bundles when the process of fusion between main bundle and group bundle was completed, (*c*) as stem strands which failed to fuse with the incoming bundles (text-fig. 4).

The principal characteristics of the bract bundles of this species were:—

(1) Well-developed midrib, which passed straight into the peduncle.

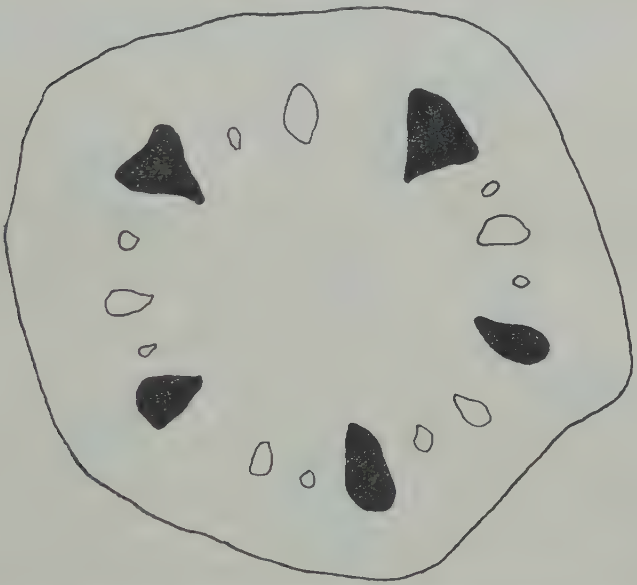
(2) Division of lateral strands, one half joining the midrib, the other joining the marginal.

(3) Fusion of marginals of adjacent bracts.

(4) The bract bundles formed the main bundles of the peduncle below the bract node.

Worsdell (**12**) records the presence at the bract node in *A. nemorosa* of several small bundles, which were observed to pass into the pith, assume an inverted orientation, and again pass outwards into the ring. This he regards as a relic of an ancestral "grandifoliate" condition, characterised by a scattered system of bundles. In the specimens described here no trace of such bundles has been found. The small xylem elements separated from the group bundles can hardly be termed "medullary bundles" or be regarded as indicating a "grandifoliate" ancestral type.

TEXT-FIG. 4.



T.S. peduncle of *A. nemorosa* below the bract node. Bract bundles shown in solid black.

Closely resembling *A. nemorosa* in the form of involucre and in the course of its vascular supply were *A. apennina* and *A. blanda*. In *A. apennina* axillary shoots were present, but no vascular tissue was differentiated in these. Small accessory marginals or laterals were observed, these linking up with the main bundles fairly high up in the petiole. The behaviour of the marginals showed more variation than in *A. nemorosa.* There was a tendency for the marginal to swing across to the lateral before this divided. When this happened the resulting bundle divided, half joining the midrib, the other half behaving as a normal marginal and fusing with that of the adjacent bract. On the other hand, the whole lateral might join the marginal, in which case half, or even the whole, of this fusion bundle later joined the midrib. With this variation, fusion of bundles was not always completed before entry into the axis (Pl. **22**, *a*).

In *A. blanda,* in addition to accessory marginals and lateral, a small strand frequently occurred on either side of the midrib and followed a course similar to that of the former strands (Pl. **23**, *a*). In the behaviour of the main bract bundles the chief points in which *A. blanda* differed from *A. nemorosa* and *A. apennina* were:—

(1) In the frequent separation of small strands from the marginals, and even from the midribs, which later linked up either with the original bundle or with the one on the other side.

(2) In a decided tendency for the fusion of lateral and marginal strands to be delayed, marginals of adjacent bracts often fusing before receiving the laterals.

In both these species the vascular ring of the axis above the bract node resembled that of *A. nemorosa*, and the rearrangement of bundles proceeded on the same lines (Pls. **22**, *b*, and **23**, *b*). The spreading out of large bundles preparatory to division was a marked feature in *A. blanda.*

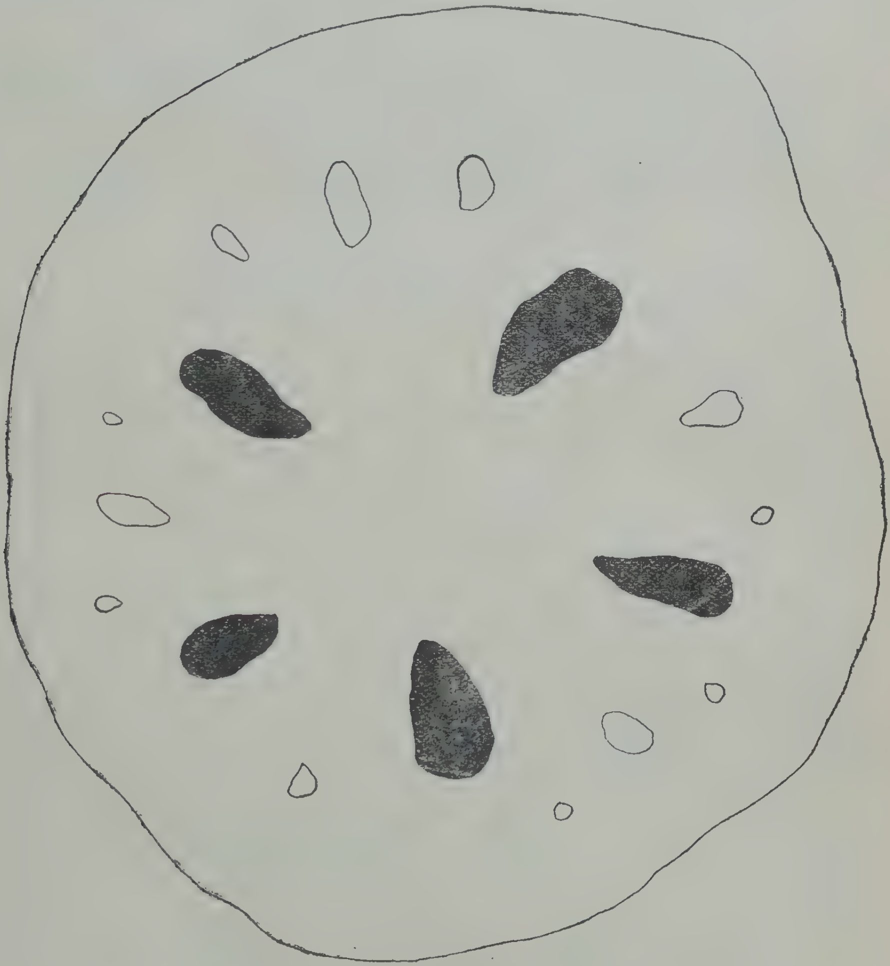
In *A. apennina* four of the incoming bract bundles, two midribs and two marginals, passed into the axis ring and formed main bundles. The fifth might be formed by a swinging across of a marginal to a midrib, or *vice versâ*, or both of these might turn in and join, enclosing the intervening stem bundles. Where fusion of marginals had not been completed in the sheathing region of the involucre, it was either accomplished as the bundles entered the axis ring, or failed to take place altogether, the independent marginals joining the group bundles of the ring. These did not differ in any marked degree from those of *A. nemorosa*, dividing and joining the bract bundles in the manner described for that species. During this process also, the separation of one or two xylem elements which passed out again in the course of half-a-dozen sections was observed.

One interesting variation in the behaviour of the incoming bundles was observed in one specimen of *A. blanda.* Here all six bundles passed into the axis ring. One midrib, however, gave off a strand on either side, and gradually became reduced until it could not be distinguished from the stem bundles.

The later course of the bundles in this species showed a very marked difference from that in *A. nemorosa* and *A. apennina.* The stem bundles gave off small strands just as, or just after, they joined the main bundles.

These strands usually joined in pairs, and then divided into two or three bundles. The main bundles, after receiving the stem strands, passed inside the vascular ring, forming a second ring, while the small outer bundles became more regularly arranged (text-fig. 5). The significance of this double ring of bundles will be considered later.

TEXT-FIG. 5.



*A. blanda.* T.S. peduncle below the bract node.

*A. silvestris* and *A. rivularis* resembled *A. nemorosa* in certain respects, although here, as usual, the petiolar reduction was accompanied by an increase in the number of bundles. In addition to midrib, laterals, and marginals, a varying number of accessory strands were present. Thus in the involucre of a large node of *A. rivularis* there might be as many as six small accessory marginals on the outer side of the main bundle. The midribs followed the usual course down to the axis, and the laterals generally divided, half joining the midrib and half the marginal (Pls. **24**, *a*, & **25**, *a*). The large number of small accessory strands tended to interrupt the regularity of the course of the main bundles, since the former frequently divided and fused among themselves before linking up with the latter, and not uncommonly one or more of the accessory marginal strands remained independent throughout. As in *A. nemorosa*, the laterals did not invariably divide, the whole bundle sometimes joining the midrib.

Divergence of marginals and fusion with those of adjacent bracts was characteristic of *A. sylvestris* and of the larger nodes of *A. rivularis*, where the involucre consisted of three bracts. It was noted that in the latter species, in the axillary shoots which bore only two hypsophylls, the marginals tended to remain distinct, even when adjacent accessory marginals joined.

Two nodes of *A. sylvestris* showed features of special interest. In one the involucre consisted of four bracts, and from the way in which the bundles linked up it would appear that three of these corresponded to the typical involucre, the fourth being associated with the axillary shoot. The accessory marginals of the bracts on either side this "extra" hypsophyll diverged and joined, passing in front of the midrib of the latter, but the resulting bundle which would in this way lie directly in front of the incoming bundles of the fourth bract died out, its place being taken by the fourth bract midrib. The adjacent marginal on one side of the "extra" bract died out, that on the other persisted as an independent bundle. The two marginals of the fourth bract diverged widely, and, passing behind several bundles of the adjacent bracts, entered the stem as independent strands (Pl. **26**).

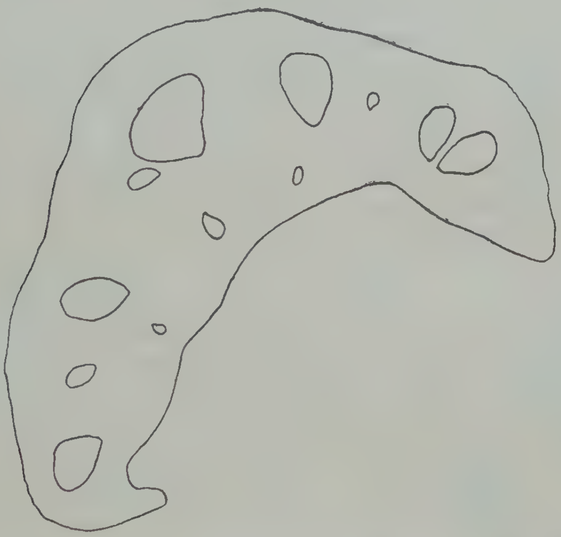
The other feature of special interest was the presence of two or three small inverted bundles in each of the three bracts of one specimen. The usual five main bundles were present, and these small inverted strands formed an inner arc. The course of the inverted bundles varied. Several were observed to die out, others passed outwards and joined a midrib, marginal or lateral bundle (text-fig. 6). Inverted bundles were not observed in the other nodes of *A. sylvestris* that were examined, and the matter requires further investigation.

One specimen of *A. sylvestris* exhibited a well-developed axillary shoot, bearing an involucre of three bracts, and a flower. At the node of this axillary shoot the entry of the bract bundles into the axis resembled *A. nemorosa* very closely. The vascular ring of the axis, containing thirteen bundles, became rearranged in the usual manner, but five gaps were formed instead of six, since the crossing over of a marginal to join a midrib was accomplished before these bundles entered the ring. The five incoming bundles passed down as usual and received strands from stem bundles. In the latter the fusion of group bundles was much less marked than in *A. nemorosa*, several retaining their identity and constituting subsidiary stem bundles. Contact strands were a characteristic feature.

The larger nodes did not show nearly such a regular course, and exhibited features not present in the smaller node. Gaps were formed in the axis ring, and as each midrib entered it usually gave off a strand from either side which passed into the ring before the bulk of the bundle, and eventually joined the stem bundle or group of stem bundles nearest to it. This separation of a small strand during entry into the axis was also observed in the case of marginal bundles (Pl. **24**, *b*).

In the large node where fusion of bract bundles was completed each of the six incoming strands passed down as a main bundle. The behaviour of the group bundles was markedly irregular. After approaching each other closely in the usual manner, one, two, or three bundles separated out and continued down the axis. In some instances strands were given off to the incoming bundles, but there was not the same out-turning of group bundles so characteristic of *A. nemorosa* and of the small node of *A. sylvestris*. As before, small strands from the main bundles assisted in the formation of the smaller bundles of the vascular ring of the peduncle.

TEXT-FIG. 6.



*A. sylvestris.* T.S. bract petiole showing inverted bundles.

The large node where four bracts were present and fusion of bundles was incomplete showed further complications, due to the increased number of bundles entering. Of the four midribs, two followed the usual course; a third, together with the marginal of the adjacent bract and the intervening stem strands, formed another main axis bundle; the fourth midrib, being carried across by an independent marginal, joined an inturning group of stem bundles and ranked as a main strand. Two marginals also constituted main bundles, and a seventh was later formed entirely from stem strands. The remaining incoming bract bundles were small independent marginals. These joined stem bundles, either entering in the middle of a bundle or at one side. In other respects this specimen resembled the one already described. Large incoming bundles gave off a strand at either side, and the stem bundles, after joining up, tended to form independent bundles rather than fuse with the main ones.

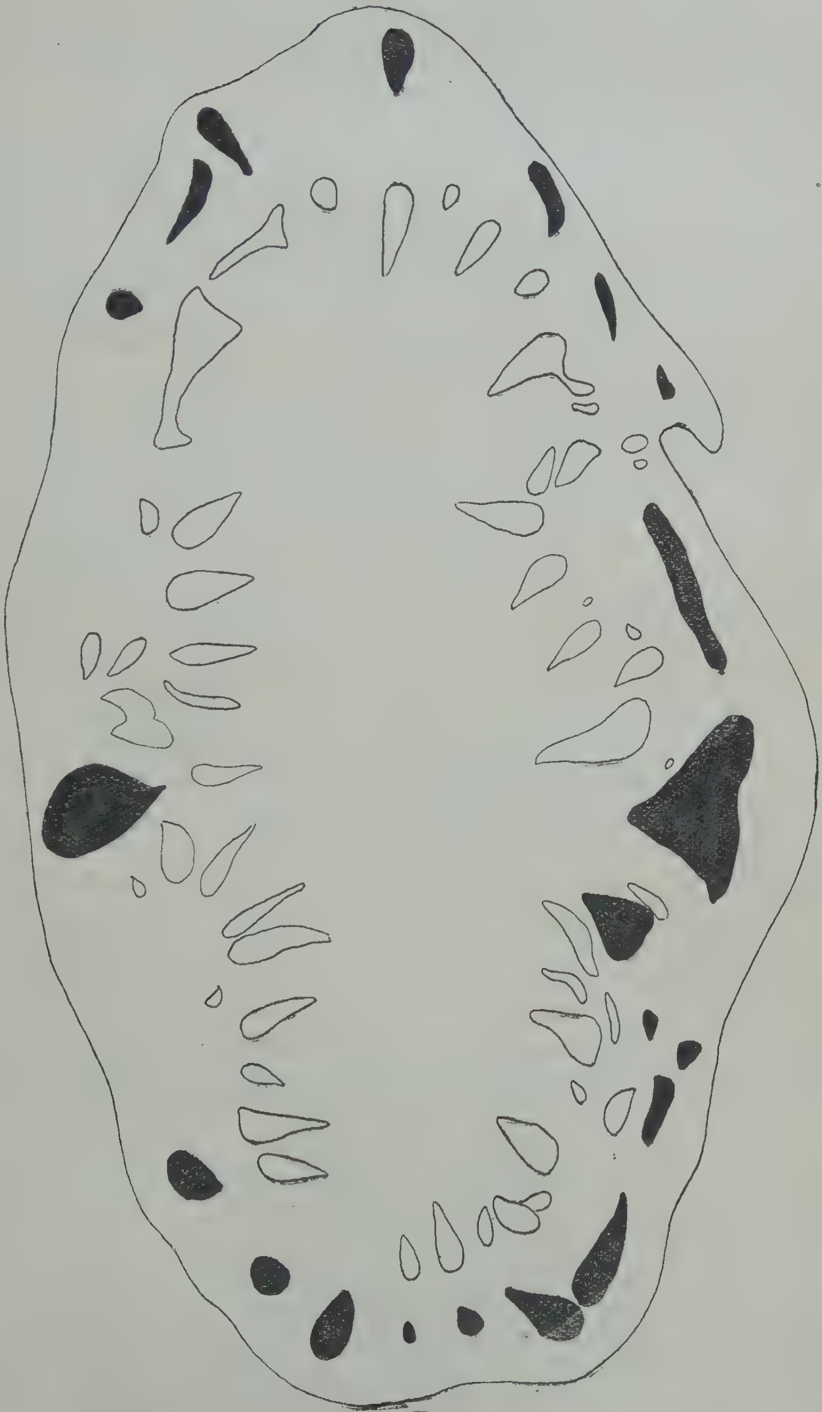
The nodes of the axillary shoots of *A. rivularis* resembled *A. sylvestris* in that all the large incoming bundles as a rule passed down the axis as main strands, and the axis bundles, though occasionally giving off strands to the incoming bundles, usually retained their identity and constituted smaller ring bundles. Thus, as a result, the vascular ring of the axis below the node consisted of a varying number of large bundles, according to the degree of fusion of the bract bundles, and of about twenty smaller stem strands, frequently arranged in groups of three between the main bundles. Small shoots present in the axils of the bracts of these nodes showed no differentiation of vascular tissue.

The main node of this specimen showed a much more complicated structure than those of the axillary shoots. At the node the first change was the opening of the central ring to receive the vascular bundles of the two axillary shoots. During this process the central ring became oval in section, and a gap was formed at either end. The curious feature of this rearrangement was that a number of small strands was given off from the bundles between the two gaps, and these, assuming an inverted orientation, passed outside the ring. No suggestion of this was observed in the smaller nodes (Pl. **25**, *b*, and text-fig. 7).

The incoming bract bundles consisted of three midribs, two large marginal bundles, and a group of four small independent marginals which had failed to link up. Gaps were formed in the irregular axis ring in the usual way, except that again small strands became separated and passed out as inverted bundles. The five large bundles entered and continued down the axis, occasionally giving off a small strand to a stem bundle. The four small bundles passed into stem strands and could no longer be distinguished.

During this process the inverted bundles underwent a slight division and fusion among themselves, and gradually assumed normal orientation. About half of these bundles joined ordinary stem strands, but the rest remained independent. As the entry of the large bundles was gradually effected, the stem bundles became arranged in two rings, the outer one consisting of small bundles, while the larger ones formed the inner ring. The

TEXT-FIG. 7.

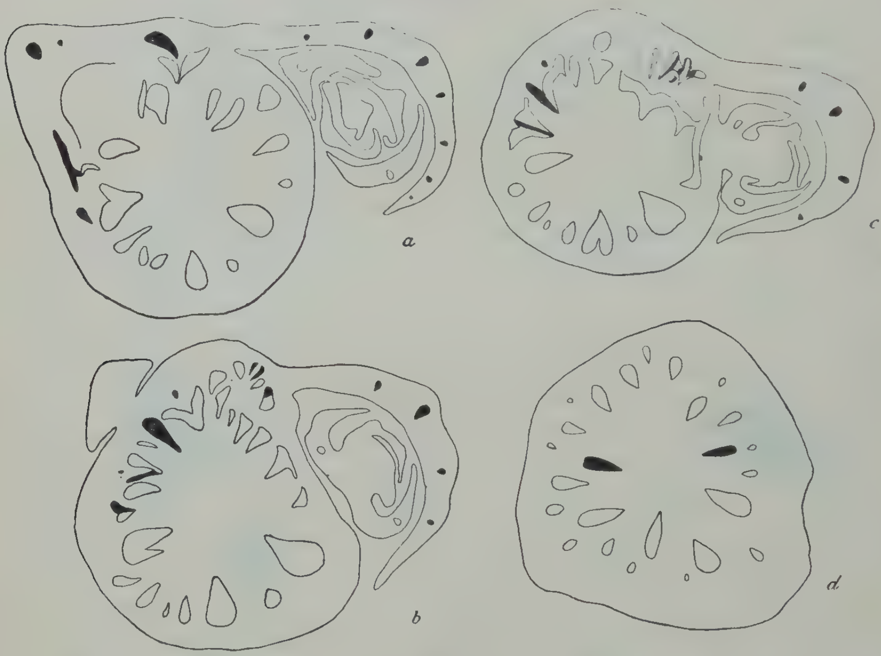


*A. rivularis.* T.S. node showing small bundles passing out of the ring and becoming inverted.

five bract bundles now passed a short distance into the pith, so that finally the vascular system of the axis consisted of three rings of bundles. The passing into the pith of the large bract bundles to form an inner ring was noted, it will be remembered, in *A. blanda* also.

*A. japonica.* Here, as in the other species described, the vascular supply of the bracts consisted of midrib, two laterals and two marginals, and a varying number of accessory strands, which in this case linked up with the large bundles before entering the axis. Typically there were two bracts at each node. The two midribs passed down as usual into the stem. The laterals divided, but the resulting strands continued to the base of the bract as independent strands, only joining the midrib or marginal very occasionally. The marginals diverged, but fusion or even close approximation of the marginals of adjacent bracts was rare (Pl. **27**).

TEXT-FIG. 8.



*A. japonica.* T.S. bract node. *a,* formation of midrib gap and passing out of stem strands; *b* & *c,* later stages in the entrance of bract bundles; *d,* below the bract node, showing the two midribs in the inner vascular ring. (Bract bundles shown in solid black.)

The vascular ring of the peduncle of a small axillary shoot contained about six or seven large bundles and an equal number of small ones. Their arrangement was slightly irregular, giving a suggestion of a double ring. Immediately above the node the bundles began to divide as usual, and, as in *A. rivularis,* strands separated and passed out of the ring. Here, however, there was one important difference. In *A. japonica* none of these bundles were observed to assume an inverted orientation, but remained endarch throughout. Several of the smaller axis bundles were seen to pass out of the ring as entire strands. As a result of this the ring became somewhat irregular, but two definite gaps were formed, one opposite each incoming midrib. These two bundles entered in the manner shown by the species described above, but the remaining bundles, of which there were a number owing to the lack of fusion between marginal and lateral strands, showed variation in their course. Several were joined by bundles which had passed out of the ring or swung across to join these. Others passed into stem strands, either at the side, at the middle, or dividing between two stem bundles (text-fig. 8).

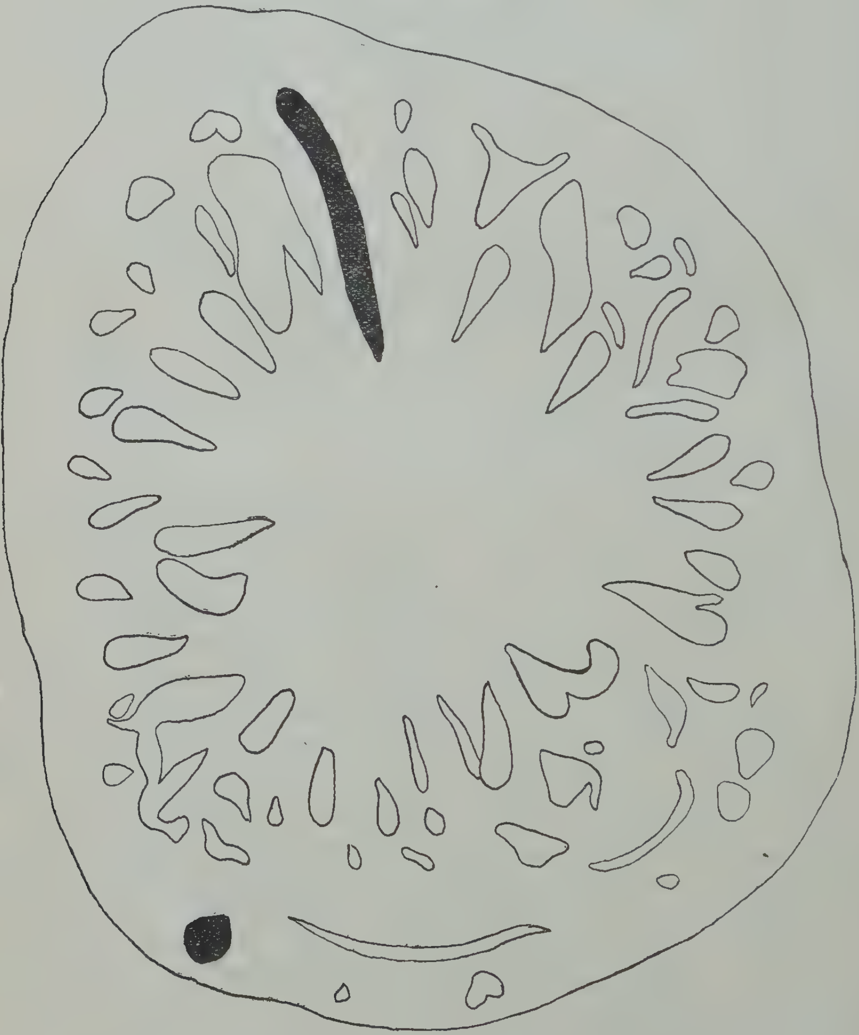
The incoming midribs sometimes received strands from the stem bundles, but there was nothing comparable to the very definite division and inturning of stem bundles which characterised *A. nemorosa*, neither did the stem bundles form definite groups, nor tend to lose their identity.

The larger axis bundles, of which there were about seven, including the two midribs, formed an inner vascular ring, smaller ones formed a second, and the very small strands, of which there were several, being a little to the outside, gave the impression of a third ring.

At the larger nodes the vascular cylinder above the involucre consisted of three rings of bundles. At the node the vascular systems of the axillary branches linked up with that of the main axis, giving rise, at this stage, to a very irregularly shaped cylinder. No large gaps were formed opposite the bract bundles, but a separation of strands allowed the midribs to enter and pass into the innermost ring (text-fig. 9). During this process small bundles passed out a short distance from each of the three rings, in the manner described for the smaller nodes. As before, these divided and fused amongst themselves and with the smaller bract bundles, which were now closely approaching the vascular cylinder. Owing to the maze of bundles at this stage it was impossible to trace the later course of the incoming marginals and laterals, and this was done only in the case of the midribs, which constituted main axis bundles. As in the smaller nodes, none of the strands which passed out from the axis rings were observed to assume inverted orientation. When the rearrangement was completed the axis exhibited a series of three rings of bundles, the larger ones, two of which were bract midribs, forming the inner ring.

Turning again to the smaller forms which exhibited a definite involucre of three bracts, *A. ranunculoides* as compared with *A. nemorosa* was characterised by a reduction of the bract petiole and a broadening of the base, and showed interesting variations from the latter type (Pl. 28, *a*). Midrib and laterals were well marked in the bract petiole, but the marginals were at this stage represented by a group of two, three, or four small bundles. Small strands accompanying the midrib and accessory lateral strands occurred, and usually joined the main bundles, but occasionally were observed to continue down as independent strands. The midrib passed down as usual, sometimes giving off small strands. The laterals divided, and in each case the inner half joined the midrib, but the behaviour of the outer half varied. This bundle frequently remained as an independent strand, receiving contributions from midrib or marginal, but sometimes passed over to join the group of marginals, which linked up to form a main

Text-fig. 9.



*A. japonica.* T.S. large node. (Bract midrib in solid black.)

bundle. As fusion between the marginals was not always complete, small accessory strands might persist. When a lateral strand joined a marginal the resulting bundle as a rule divided, the inner half behaving as an independent lateral, the outer half as an ordinary marginal. Approximation and fusion of marginals of adjacent bracts were accomplished, and were sometimes complicated by the division of marginal bundles. In a few instances this division was at right angles to the ordinary plane of division.

The rearrangement at the node differed in several respects from that of *A. nemorosa*. The stem bundles spread out as in *A. blanda*, but gaps were formed opposite the midribs, before those for the marginals. The small bundles of the axillary shoots joined the stem bundles on either side of the midrib gap. Almost immediately afterwards the large incoming bract bundles entered, following the usual course and constituting the five main axis bundles (Pl. **28**, *b*). The group bundles approached each other closely during this process, but a separation of bundles then took place to allow the small bract bundles to enter. These joined ring bundles, but occasionally an independent lateral continued down as a subsidiary stem bundle. The later stages of re-arrangement followed the *A. nemorosa* type closely, even to the separation of one or two xylem elements and the formation of contact strands.

*A. coronaria* with a sessile involucre exhibited an increase in the number of accessory bundles and in the degree of independence between these (Pl. **29**, *a*). The midribs followed the usual course ; the laterals, which were very large bundles, as a rule divided, but occasionally an entire lateral was observed to swing over to the midrib. The tendency for lateral strands to become independent bundles, which was noted in *A. ranunculoides*, was still more marked in *A. coronaria*. Thus in one specimen the inner half of a divided lateral was seen to continue down to the axis instead of joining the midrib ; in another an undivided lateral, after giving off a very small strand on either side, behaved similarly, and in several the outer half of a divided lateral was observed to remain independent, although others joined marginals as usual.

The only noteworthy point in the behaviour of the groups of marginals was that the chief marginal sometimes passed into the axis as an independent strand, while the accessory marginals joined those of the adjacent bract. Fusion of adjacent marginals was not always completed, several small bundles often retaining their independence or being separated after fusion.

The vascular ring of the axis consisted of about twelve large bundles, these alternating with one, two, or three smaller ones. Rearrangement proceeded as usual, the midrib gaps being particularly well marked. In their behaviour, the marginal and independent lateral strands showed interesting departures from those of the species previously described. If fusion of marginals in the involucral base was fairly complete, these behaved as usual, two constituting main bundles, the others combining with a midrib to form a third. If, on the other hand, the marginals failed to join to form a large bundle, two or three independent lateral and marginal strands would link up, the resulting bundle ranking as a main strand. In each example observed, the bracts contributed five main axis bundles, as in *A. nemorosa* (Pl. **29**, *b*). The remaining bract bundles often passed into the ring and down as subsidiary bundles, but sometimes were received into the middle or at one side of stem bundles.

The groups of stem bundles spread out in the usual manner. As a rule, the central portion of the group continued as a large subsidiary bundle, the outer portions separating to join the large incoming strands. Two or three small bundles were frequently formed on either side of these subsidiary ones by the separation of elements from main or subsidiary bundles.

The bundles now became arranged in three rings, the inner one consisting of five main bundles, a second of the large subsidiary bundles, some bracteal in origin, and the third of numerous small bundles in groups of two or three.

*A. Pulsatilla.* It was usually possible in *A. Pulsatilla* to distinguish the bract from the bracteoles by reason of its larger size and complicated vascular system, the number of accessory bundles being as high as seventeen or eighteen (Pl. **30**, *a*). The midribs did not exhibit any features of special interest. Occasionally the laterals divided, sending a strand to the midrib and to the marginal; but either of the divided lateral strands might constitute an independent bundle. Quite often a lateral failed to divide, the entire strand passing down to the axis, and sometimes receiving a strand from a marginal or midrib. The chief marginal, on the other hand, was observed in several cases to divide, half swinging across to the lateral, half joining the subsidiary marginal group. Thus in these latero-marginals the parts played by lateral and marginal were exactly the reverse of those in latero-marginals of the "*nemorosa* type." Fusion of accessory marginals of adjacent bracts was accomplished, and sometimes this fusion bundle was joined by the chief marginal, which at other times remained independent.

In the vascular ring of the axis above the node there were about twelve large bundles and three or four smaller ones. During rearrangement practically all these bundles divided so that a gap was formed for each bract bundle (Pl. **30**, *b*). These incoming strands entered the ring, and almost all of them passed straight down the axis. Very small independent laterals or marginals might join stem strands or large bract bundles, but there was no linking up of midrib and marginal. No distinction could be drawn between midribs, laterals, and marginals in their behaviour from this point, each bract bundle constituting a main axis bundle.

The course of the stem bundles was very characteristic. They formed irregular masses between the bract bundles, before dividing into two bundles which diverged and joined the main strands. "Contact strands" were only occasionally formed. In *A. Pulsatilla*, therefore, instead of the ring of five large bundles which has been found to be a constant feature of the peduncle in the majority of species of *Anemone* examined, a ring was formed consisting of a varying number of bundles of approximately equal size, the number depending on that of the incoming bract bundles.

*A. fulgens.* The external differentiation into bract and bracteoles was not accompanied by any marked anatomical distinction. Midribs, laterals, and marginals were present as usual, and a few accessory strands. Division of laterals was frequently observed, the resulting strands resembling those of *A. coronaria* and *A. Pulsatilla* in their behaviour, and even showing a more marked tendency to remain independent (Pl. **31**, *a*). The accessory marginals linked up with the chief marginals, which diverged and fused with those of the adjacent bract. The process of fusion was completed as the bundles were about to enter the axis ring.

The vascular ring of the peduncle consisted of about twelve main bundles alternating with the groups of one, two, or three subsidiary ones. A gap was formed at the node opposite each incoming bundle. Nearly all these bundles entered the ring and continued their course down the axis, but only five main strands were formed (Pl. **31**, *b*). These might be formed by midribs and marginals as in *A. nemorosa*, but this was not invariably so. In one instance a fusion of a midrib, a marginal, and a lateral to form a main bundle was observed; in another a main bundle was formed entirely by a lateral, while in a third one was formed almost entirely by the linking up of several stem strands, only a very small portion being contributed by bract bundles. In these cases the midrib or marginal, which usually ranked as a main strand, remained as a subsidiary bundle.

The stem bundles formed irregular masses, strands of which turned out to join the bract bundles, while the middle portion continued down as a subsidiary bundle. As in other cases, small strands frequently separated just before or just after fusion with the bract bundles. The five main bundles passed slightly into the medulla; so that here again a double ring of bundles was formed below the node.

*A. palmata.* The bract bundles differed from those of *A. fulgens* in their later course only. The tendency for the main marginal to remain distinct and to contribute to independent lateral strands was a marked feature (Pl. **32**, *a*). The accessory marginals linked up either with the chief marginal or amongst themselves to form one fairly large strand. *A. palmata* differed in one very important respect from *A. fulgens*, and indeed from all the smaller species so far described. The marginals diverged a little, but there was no fusion between marginals of adjacent bracts.

The vascular ring above the node consisted of about twelve large bundles alternating with a number of small ones. The first change was the opening of the ring to receive the bundles from the two small axillary shoots which were present. Three well-marked gaps were then formed, one opposite each incoming midrib, which on entering became a main axis bundle (Pl. **32**, *b*). Two marginals also constituted main bundles, and the rest of the bract bundles passed down as subsidiary strands or joined axis bundles. The groups of stem bundles, meanwhile, approached each other and then separated into several strands, some passing over to the bract bundles, but the majority continuing down as subsidiary axis bundles.

*A. angulosa.* The vascular bundles of the small sepal-like bracts consisted of midrib, laterals and marginals, and usually two small accessory midribs in each bract, which linked up with the midrib or continued down as separate strands (Pl. **33**, *a*). The marginals swung across to the laterals, which did not divide. After receiving the marginals, the laterals diverged a little from the midrib, and each entered the axis as an independent bundle. Very rarely the marginals failed to join the laterals, and passed into the peduncle independently.

In the peduncle, above the node, the vascular ring contained from nine to twelve large bundles and several smaller ones. During the rearrangement three gaps were formed, one opposite each incoming midrib, which after entering constituted a main bundle, and shortly after minor gaps appeared opposite the laterals (Pl. **33**, *b*). In one specimen a lateral was seen to form a main axis bundle; but in many cases the lateral divided, two resulting strands diverging and joining the bundles on either side, while in yet other cases the lateral passed over to a ring bundle without dividing. The stem bundles remained distinct except for the fusion required to enclose the incoming laterals. Two stem bundles continued down as main strands, bringing the number up to five. Where a lateral became a main bundle, only one stem strand ranked as such. The remaining bundles divided and joined the main strands. Occasionally the central portion continued as a subsidiary bundle; but true "contact strands" were not formed, as the stem strands usually remained distinct throughout. One of the most striking features of this species when compared with those already described was that the entry of the bract bundles caused far less disturbance of the vascular system of the peduncle.

*A. Hepatica.* In the bracts there was a very close resemblance between the vascular system of this system of this and the previous species. Indeed, the only point of difference was that in *A. Hepatica* the marginals were smaller and more insignificant, and might be absent altogether (Pl. **34**, *a*).

The axis ring contained about twelve large bundles and several smaller ones, and the rearrangement at the node followed the course described for *A. angulosa*, not differing in any respect except that the division of the laterals after entering the ring took place more frequently (Pl. **34**, *b*).

*Ranunculus Ficaria.* The vascular supply of the sepals consisted of midrib, laterals and marginals, and several accessory bundles which linked up the main strands (Pl. **35**, *a*). The midribs passed down to the peduncle. The marginals either swung across to the laterals or remained as independent bundles. The laterals diverged slightly and entered the axis, there being no suggestion of fusion of bundles of adjacent sepals. The resemblance between the vascular system of the sepals of *Ranunculus Ficaria* and the bracts of *A. angulosa* and *A. Hepatica* is obvious.

The rearrangement of the vascular ring of the axis caused by the entry of the petal bundles was not yet fully completed, so that it was represented by about twelve irregularly-arranged strands. The sepal bundles entered between these bundles, and no distinction was observed between the part played by midribs and that by laterals. Almost without exception the sepal bundles divided, the two halves joining the stem bundle on either side. Occasionally an incoming bundle entered at one side or in the middle of an axis bundle (Pl. **35**, *b*).

The peduncle bundles now linked up to form a vascular ring, consisting usually of five main bundles and several smaller ones.

One specimen examined showed an interesting variation. Here an extra leafy sepal occurred in a position similar to that of the bracts of *A. Hepatica.* This "sepal" contributed one bundle to the peduncle, and its course was as follows:—A main axis bundle divided, and the sepal bundle entered in the gap so formed and continued down the axis without dividing. The two halves of the divided bundle turned in to the incoming bundle in the same way that the stem strands in *A. nemorosa* turned in to join the incoming bract bundles.

*Eranthis hyemalis.* Apart from the presence of a varying number of small accessory strands which linked up with the main bundles, the bracts of *Eranthis hyemalis* showed a very striking resemblance to the bracts of *A. nemorosa* in the course of their vascular bundles. Midribs, laterals, and marginals behaved in the manner described for that species of *Anemone,* and fusion between marginals of adjacent bracts was completed (Pl. **36**, *a*).

Although an internode between perianth and involucre could not be distinguished, the vascular strands of the axis had settled down, after the entry of the perianth bundles, into a ring of about fourteen regularly-arranged bundles. These divided and moved to one side, leaving well-marked gaps opposite the incoming bundles. Each of these entered the ring and continued down as a main bundle (Pl. **36**, *b*). A very characteristic feature was the separation of a small strand from each side of the incoming bundle, these small strands frequently being the first part of the bundle to enter. They subsequently joined the nearest stem bundle.

The stem bundles remained distinct, and did not contribute in any way to the six main bundles. They divided and joined up amongst themselves, with the result that between each pair of main bundles there were usually three stem strands.

## Discussion.

From the foregoing account it will be clear that the difference in the form and position of the bracts of these species of *Anemone* is accompanied by well-defined anatomical variations. Certain of these variations in the vascular supply appear to be directly correlated with the form and function of the bracts, since the vascular supply is determined to a certain extent by the physiological requirements of the plant.

The chief interest of the bracts lies in the behaviour of the lateral and marginal bundles. In those species typified by *A. nemorosa* the laterals divide, the outer half swinging across to the marginal, which then fuses with that of the adjacent bract. This is characteristic also of the species such as *A. sylvestris* and *A. rivularis,* where well-developed axillary shoots normally occur. In *A. japonica*, on the other hand, though the laterals divide, there is no fusion either between lateral and midrib, lateral and marginal, or marginals of opposite bracts. This may be correlated with the fact that in this species there is no suggestion of involucre formation, the bracts being simply leaves on the peduncle, in the axils of which shoots arise.

In *A. coronaria, A. fulgens,* and species resembling them in the reduction of lamina and petiole, and the broadening of the bract base, there is a decided tendency for laterals and marginals to enter as independent bundles, while in *A. Hepatica* the parts played by lateral and marginal in *A. nemorosa* are completely reversed. Here the marginals swing over to the laterals, which then diverge slightly, but, unlike the marginals of *A. nemorosa*, do not link up with the corresponding bundles of the adjacent bracts. The striking resemblance between the course of the bundles in the bracts of *A. nemorosa* and of *Eranthis hyemalis*, and that between the bract bundles of *A. Hepatica* and the sepal bundles of *Ranunculus Ficaria*, needs no further emphasis.

At the bract node the importance of the part played by the incoming bundles in the vascular ring of the axis varies according to the degree of development of the involucral leaves. Of the species examined, *A. japonica* appears to stand apart from the rest in several respects. The vascular bundles of the sessile bracts show little fusion amongst themselves, and very rarely with those of the other bract, which arises at the same node. The midrib alone of the incoming bundles constitutes a main axis bundle.

In smaller forms, where branching is restricted or absent and a three-leaved involucre is present, interesting variations in the course of the bract bundles occur. Where the involucre is indistinguishable from the foliage leaves in size and form (e.g., *A. sylvestris, A. nemorosa*) the bracts function as foliage leaves and the vascular supply is of corresponding importance, the bundles being large and dominating the vascular system of the peduncle. The midribs are prominent bundles; the marginals of adjacent bracts link up to form bundles of equal importance, and each of these six bundles may constitute a main bundle of the peduncle.

Reduction of petiole and lamina and the broadening of the base to form a more efficient sheathing organ reduces the photosynthetic capacity of the involucre to a certain extent. Bract bundles still form main axis strands; but the bundles of the peduncle take a more prominent part, constituting independent subsidiary bundles in addition to contributing to the main strands. The bracts here take on the more typical characteristics of hypsophylls, showing, for example, a decided tendency to parallel venation, as in *A. coronaria, A. Pulsatilla,* and an increase in the number of accessory strands. With the broad bases the linking up of marginal and lateral bundles is carried out to a far less extent than in *A. nemorosa.* The midribs behave as in the latter species; but while fusion between the accessory marginals of adjacent bracts takes place, the laterals tend to remain separate, and undergo division resulting in a large number of small strands, each of which enters the axis as an independent bundle. These modifications accompanying the reduction of the lamina and the broadening of the base are of special interest in view of the "Phyllode Theory" put forward by Arber (1).

In *A. fulgens* and *A. palmata* the bracts exhibit a still more reduced lamina, and the "hypsophyll characteristics" are more marked. The bract bundles play an important part in the formation of the vascular ring of the axis; but the bundles of the peduncle are not only concerned in the formation of subsidiary strands, but may occasionally form main axis bundles.

In *A. angulosa* and *A. Hepatica* the change from a condition in which the vascular system is dominated by that of the involucre to one in which the latter plays a minor part is becoming an accomplished fact, and the rearrangement of axis bundles to allow of the entrance bract bundles does not result in so marked a disturbance of the vascular ring. The midribs still play an important part; but here the peduncle bundles invariably form one or two of the five large bundles, the remaining bract bundles joining the nearest axis strands, either passing in as complete strands or dividing or sending a strand to the axis bundle on either side.

It is only one step further to the condition existing in *Ranunculus Ficaria* in which the midribs, laterals, and marginals of the sepals divide and join the axis bundles, these then linking up to form the five main bundles.

A comparison of *Eranthis hyemalis* with the species of *Anemone* just reviewed and with *Ranunculus Ficaria* yields suggestive results. The involucral bracts of *Eranthis hyemalis* agree with those of *A. nemorosa* in being similar to the foliage leaves in size and form and presumably in function; but they differ markedly in position, being situated immediately beneath the perianth. In essentials the behaviour of the bract bundles of *Eranthis hyemalis* does not differ from that of the bract bundles of *A. nemorosa,* since the strands are large and assume the part of main strands in the vascular ring of the axis. Thus it would appear that the change observed in the type of vascular system in the various species of *Anemone* is more clearly associated with the change in function of the bracts from that of a foliage leaf to that of a purely protective organ than with the change in position. It may be noted that in one specimen of *Ranunculus Ficaria*, in which an extra leafy sepal was present, the single bundle which entered from this sepal passed down the peduncle as a main bundle, forming a striking contrast to the course usually taken by sepal bundles.

In the majority of species of *Anemone* examined, the peduncle below the bract node exhibits five main strands and a varying number of smaller ones. In many species these bundles form a ring, but in *A. blanda* and *A. fulgens* the five main bundles pass slightly into the middle, and in *A. japonica*, *A. rivularis*, and *A. coronaria* the bundles form three series, the main bundles constituting the inner ring. Worsdell (**12**) has recorded the existence of medullary strands and of inverted cortical bundles in some members of the Ranunculaceæ, and regards these as relics of a scattered bundle condition which he considers to be the ancestral type not for the Ranales alone but for Angiosperms as a whole.

On this view the ancestral type was of "grandifoliate" habit, the scattered vascular system of the petiole dominating the vascular system of the stem, which would thus be of the scattered bundle type. The change from the "grandifoliate" to the "parvifoliate" habit is believed to have led to a change in the vascular system, the bundles becoming pressed outwards and ultimately arranged in a single ring, while the inverted cortical bundles and the medullary strands remain as persistent vestiges of the outer and inner series.

In one case only among the species of *Anemone* examined have small inverted bract bundles, which might be regarded as traces of a scattered bundle system, been observed (*A. sylvestris*). In the larger nodes of *A. rivularis* small stem strands were seen to separate and to pass out of the ring, assume inverted orientation, and, later, after dividing and fusing amongst themselves, to re-enter as bundles with normal orientation. A similar phenomenon, but without inversion of orientation, was also noted in *A. japonica*. The true significance of this process is not clear; but it appears highly improbable that it represents a vestige of an ancestral scattered bundle system, since the bundles which pass out are of peduncle and not of bracteal origin.

With regard to medullary bundles, the evidence obtained in the present investigation is not sufficient to warrant a detailed discussion of Worsdell's theory; but two points may be noted:—

(*a*) In a case like *A. japonica* or *A. coronaria*, where the inner ring consists of the main axis strands, the transition from a scattered system of bundles to a single ring would hardly result in vestigial medullary strands. In species where the single ring is characteristic it is these large bundles which form the main vascular tissue.

(*b*) The medullary strands in *Anemone* are not invariably leaf-traces, since in *A. fulgens* one of the peduncle bundles was observed to constitute a member of the inner ring.

An alternate explanation of medullary bundles has been suggested in the case of certain orders. Thus in Begoniaceæ the medullary vascular system of the stems of certain species is regarded as a result of the formation of tubers and rhizomes which increase the demands made on the conducting system for collecting and redistributing reserve material (**4**). If this were the explanation in the case of species of *Anemone*, it is difficult to see why the phenomenon should make its appearance in a few species only.

In *A. japonica* and *A. coronaria*, where the number of bundles below the bract node is large, the double ring of bundles might be regarded as a means to prevent overcrowding. This explanation, however, would not hold good for *A. blanda* and *A. fulgens*, where the number of bundles is not sufficiently large to bring about any suggestion of overcrowding. It is hoped that the significance of this scattered type of vascular system may be indicated by further investigation.

The study which has been made of the vascular anatomy of the bracts and of the bract nodes of these species of *Anemone* appears to support the view that the bracts of *A. Hepatica* and the calyx of *Ranunculus Ficaria* are homologous structures. If this were so, then it is conceivable that the bracts of *A. hepatica* and the calyx of species of *Ranunculus* other than *Ficaria* may also be homologous.

While realising that in many cases part of the so-called "perianth" of flowers may arise by the sterilisation of stamens, it is considered that the results obtained in the present investigation support the view expressed by Goebel (**3**) and by Prantl (**6**) that bracts may also take part in the development of perianth so that this structure may in one flower have two distinct and totally different origins. There appear to be no real grounds for limiting the development of petaloidy to any one set of organs of the flower axis, and it seems probable that a part of the perianth, the original function of which would be at least partly that of protection, may be of bracteal origin.

## SUMMARY.

1. The form and position of the bracts of various species of *Anemone* are described, and these are compared with the bracts of *Eranthis hyemalis* and with the sepals of *Ranunculus Ficaria*.

2. A detailed account is given of the vascular supply of the bracts of species of *Anemone* and of the part played by the bract bundles on entering the axis.

3. Where no definite involucre is formed (*A. japonica*), there is little fusion between the bract bundles, and on entering the axis ring, only the midrib forms a main bundle. In species resembling *A. nemorosa* with a leafy involucre the characteristic features are :—

(*a*) Division of lateral bundles, one half joining the midrib, the other half swinging over to the marginal.

(*b*) Fusion of marginals of adjacent bracts so that in all six large bundles enter the axis.

(*c*) The vascular ring on the axis below the node consists of five large bundles, all of bracteal origin, and of several smaller ones.

Species with an involucre of sessile bracts with reduced lamina and broad base (*A. coronaria, A. fulgens*) show a tendency to parallel venation, an increase in the number of bract bundles, lack of fusion between lateral and marginal ; but the vascular system of the axis is still dominated by that of the involucre.

In *A. angulosa* and *A. Hepatica*, where the reduction of the lamina of the involucral leaves results in a calyx-like structure, there is no fusion between marginals of adjacent bracts ; the part played by lateral and marginal in *A. nemorosa* is completely reversed—although the midribs still become main axis strands, the entry of the bract bundles causes relatively little disturbance of the axis ring, and peduncle bundles become main strands, while lateral bundles from the bracts show a tendency to divide.

4. The course of the sepal bundles of *Ranunculus Ficaria* resembles that of the bract bundles of *A. Hepatica* very closely ; but here all the bundles entering the axis ring play a subsidiary part, and as a rule divide.

5. The vascular supply of the bracts of *Eranthis hyemalis* resembles that of *A. nemorosa* in all essentials.

6. The variations in vascular anatomy are considered in relation to the difference in function of the bracts.

7. The significance of the double ring of bundles which occurs in several species of *Anemone* is discussed; but the evidence obtained in this investigation is regarded as insufficient to be in any way conclusive.

8. The vascular anatomy of the bracts and the bract node of these species of *Anemone* appears to support the view of the homology of the involucre of *A. Hepatica* and the calyx of *Ranunculus Ficaria*.

I wish to express my thanks to Dr. H. S. Holden, who suggested this investigation, and both to him and to Miss Bexon, for their kindly help and criticism.

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## EXPLANATION OF THE PLATES.

### PLATE 21.

*A. nemorosa.* *a,* the course of the vascular bundles of the bract; *b,* the course of bract and peduncle bundles at the node. In this and the succeeding diagrams the midribs are shown in heavy red, laterals light red, marginals broken red, accessory bundles broken black, peduncle bundles black.

### PLATE 22.

*A. apennina.* *a,* vascular bundles of the bracts; *b,* of the bract node.

### PLATE 23.

*A. blanda.* *a,* vascular bundles of the bracts; *b,* of the bract node.

### PLATE 24.

*A. sylvestris.* *a,* vascular bundles of the bracts ($x$, inverted bundles); *b,* of the bract node.

### PLATE 25.

*A. rivularis.* *a,* vascular bundles of the bract; *b,* of the bract node ($x$, bundles which pass out of the ring, assume inverted orientation, and later, assuming normal orientation, re-enter).

### PLATE 26.

*A. sylvestris.* Vascular bundles of bracts of four-leaved involucre.

### PLATE 27.

*A. japonica.* Vascular bundles of bract.

### Plate 28.

*A. ranunculoides.* *a*, vascular bundles of the bracts; *b*, of the bract node (*x*, bundles from axillary shoot).

### Plate 29.

*A. coronaria.* *a*, vascular bundles of the bracts; *b*, of the bract node.

### Plate 30.

*A. Pulsatilla.* *a*, vascular bundles of the bracts; *b*, of the bract node.

### Plate 31.

*A. fulgens.* *a*, vascular bundles of the bracts; *b*, of the bract node.

### Plate 32.

*A. palmata.* *a*, vascular bundles of the bracts; *b*, of the bract node (*x*, bundles of axillary shoots).

### Plate 33.

*A. angulosa.* *a*, vascular bundles of the bracts; *b*, of the bract node.

### Plate 34.

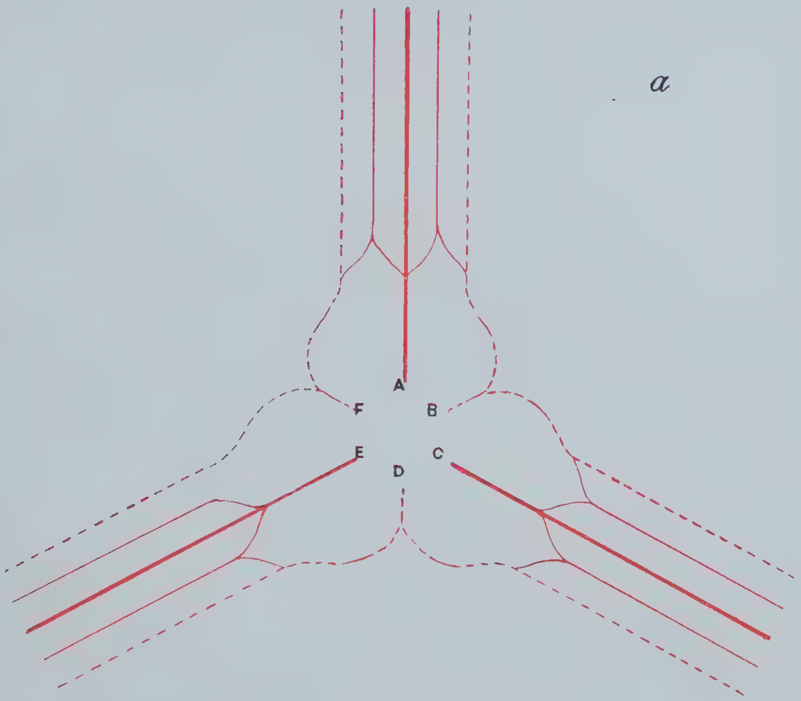
*A. Hepatica.* *a*, vascular bundles of the bracts; *b*, of the bract node.

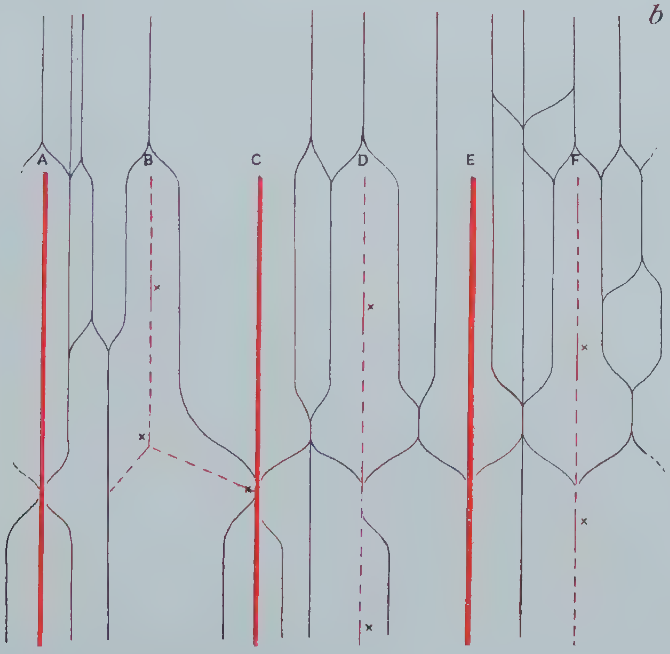
### Plate 35.

*Ranunculus Ficaria.* *a*, vascular bundles of the sepals; *b*, of the sepal node.

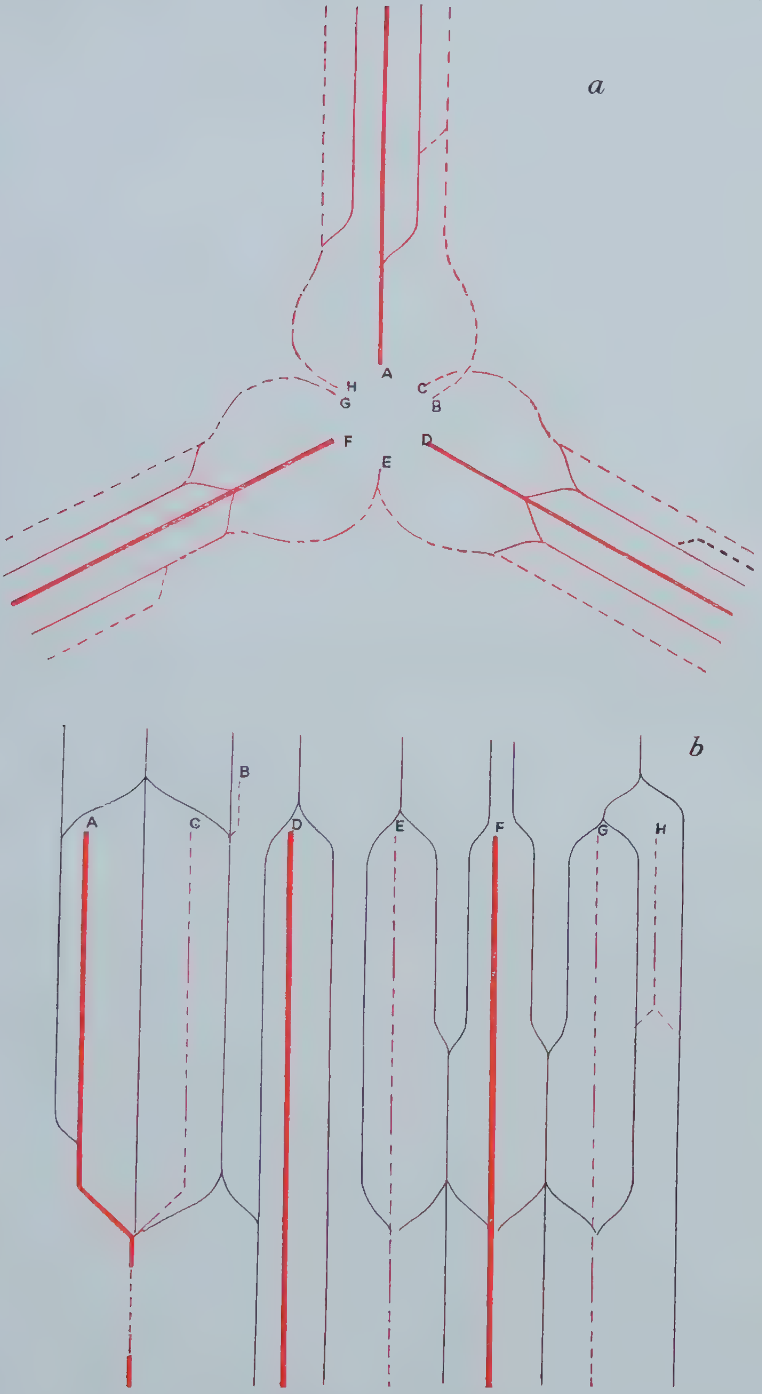
### Plate 36.

*Eranthis hyemalis.* *a*, vascular bundles of the bracts; *b*, of the bract node.

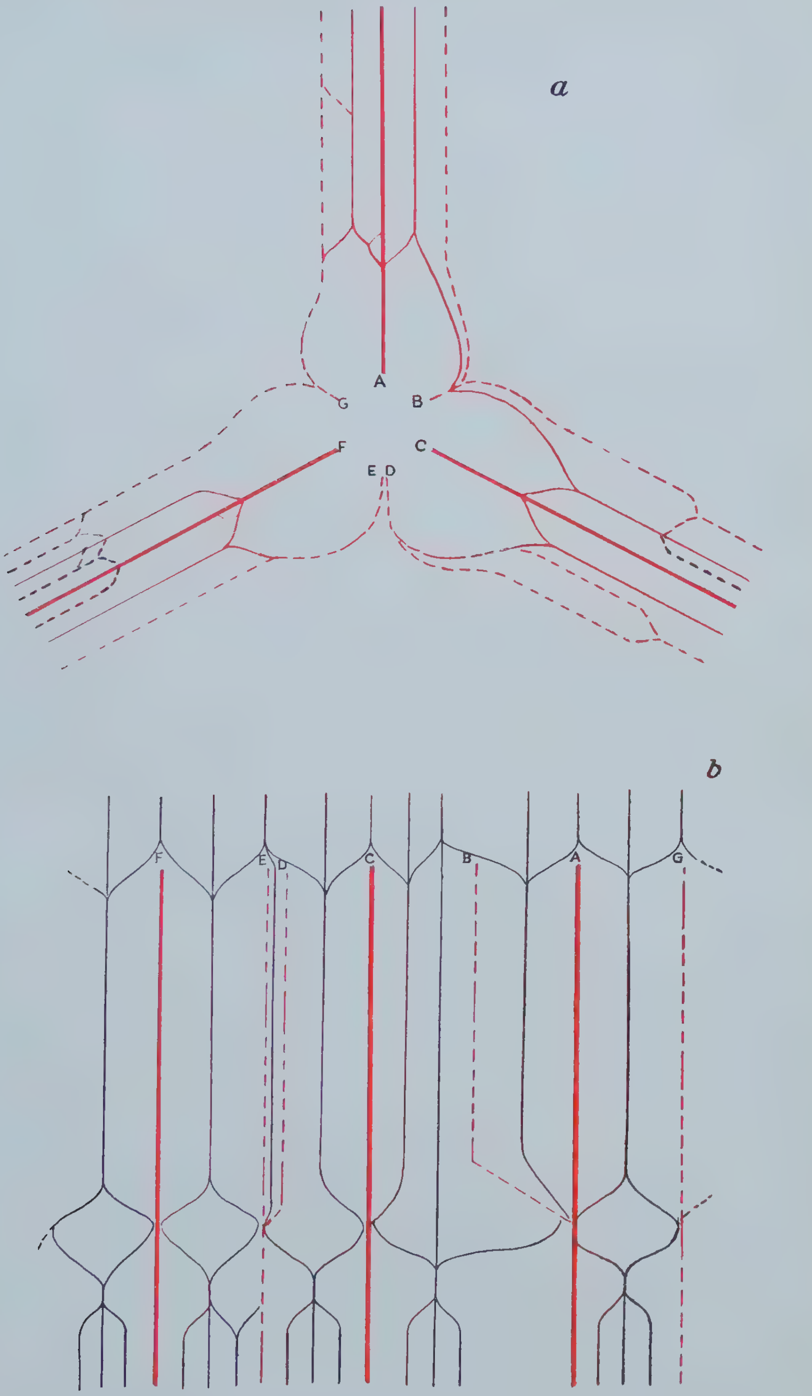




ANEMONE NEMOROSA.



ANEMONE APENNINA.



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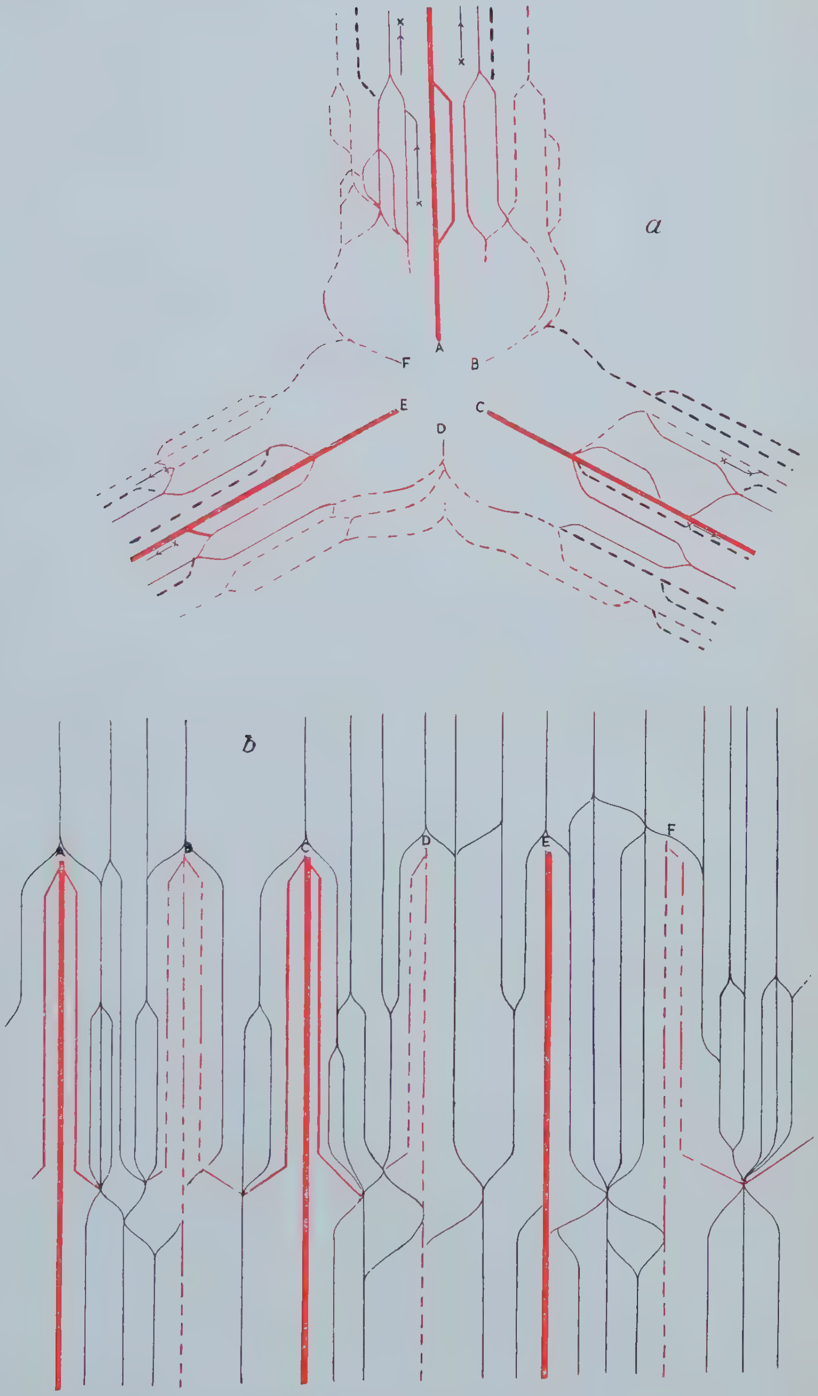

ANEMONE SYLVESTRIS.

CHESTERS.

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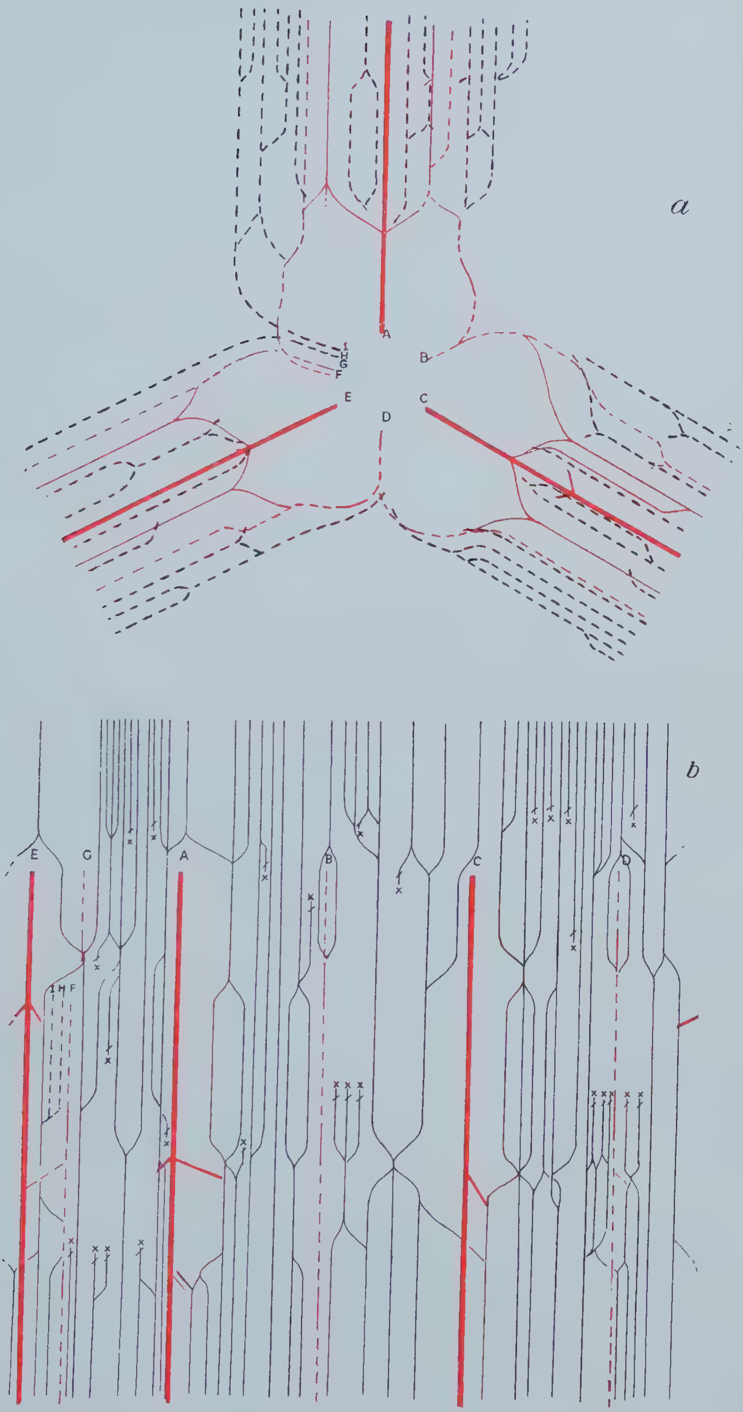

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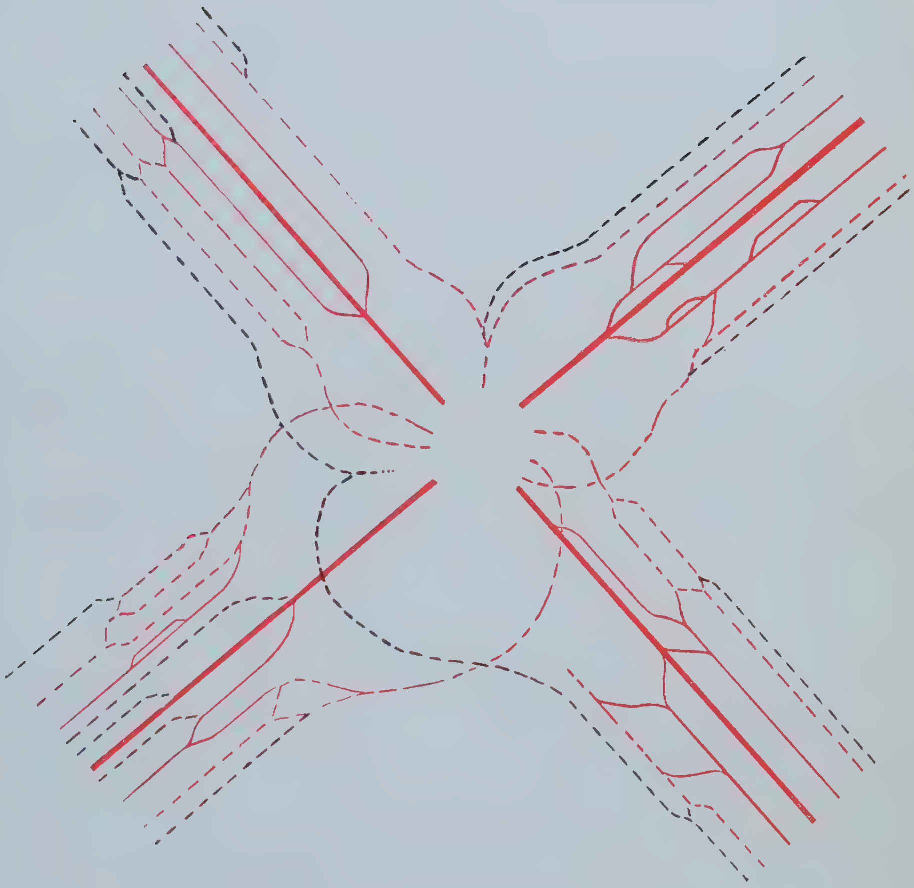

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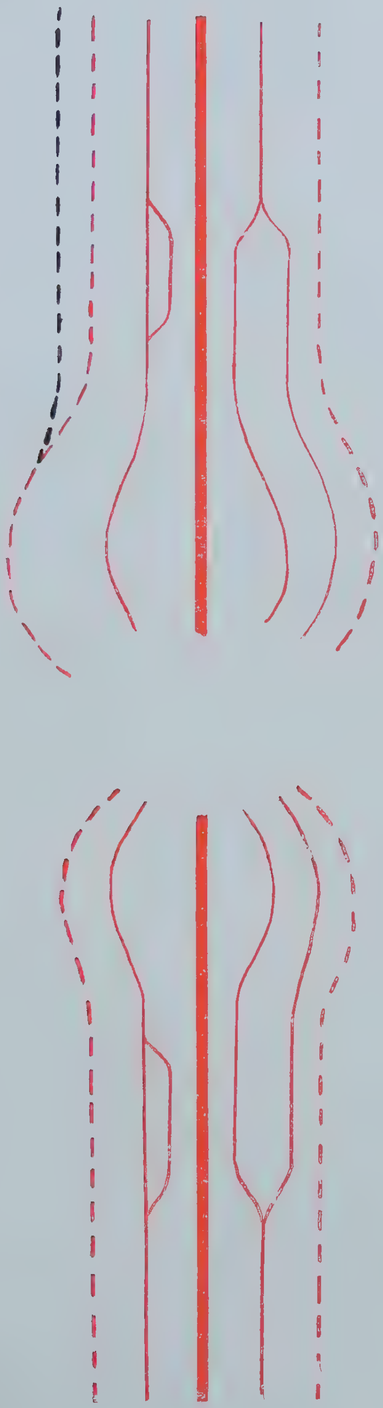

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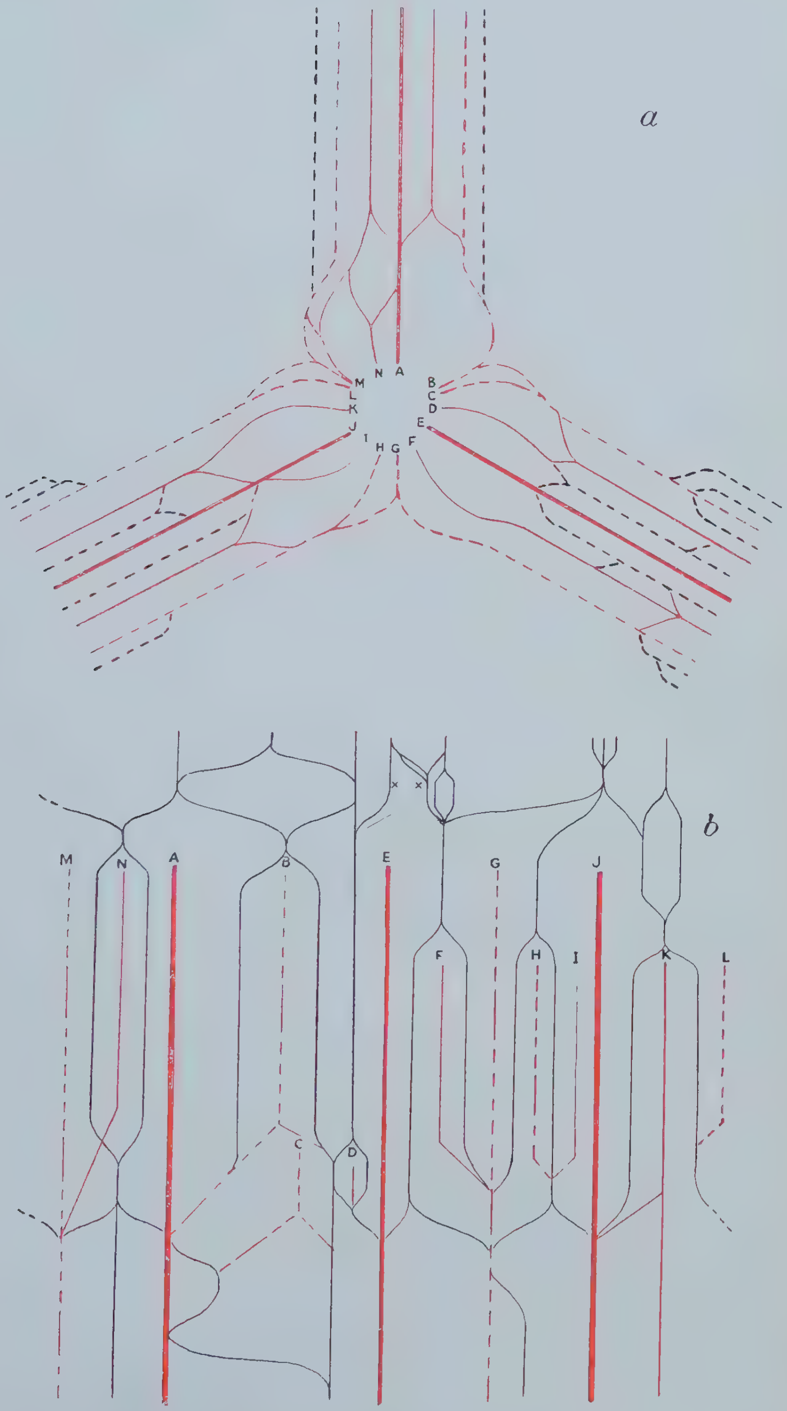

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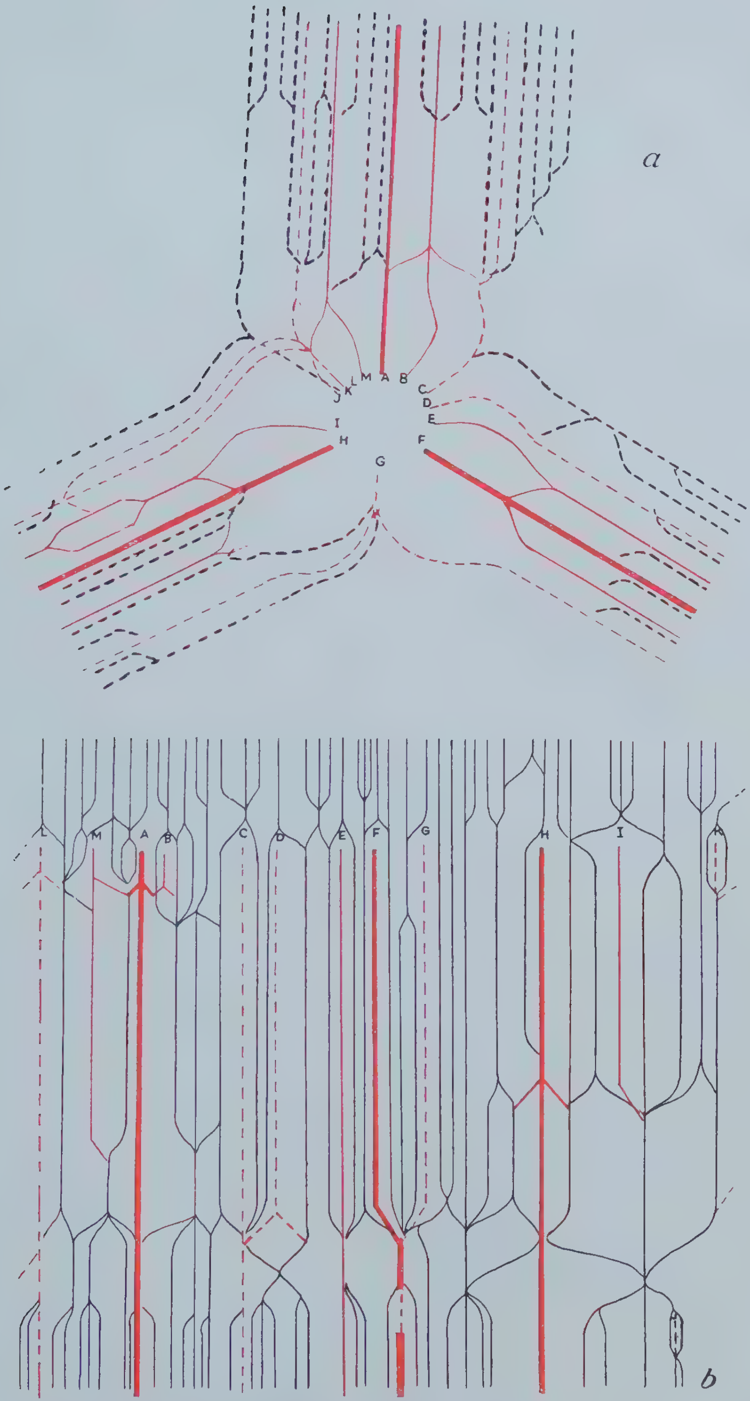

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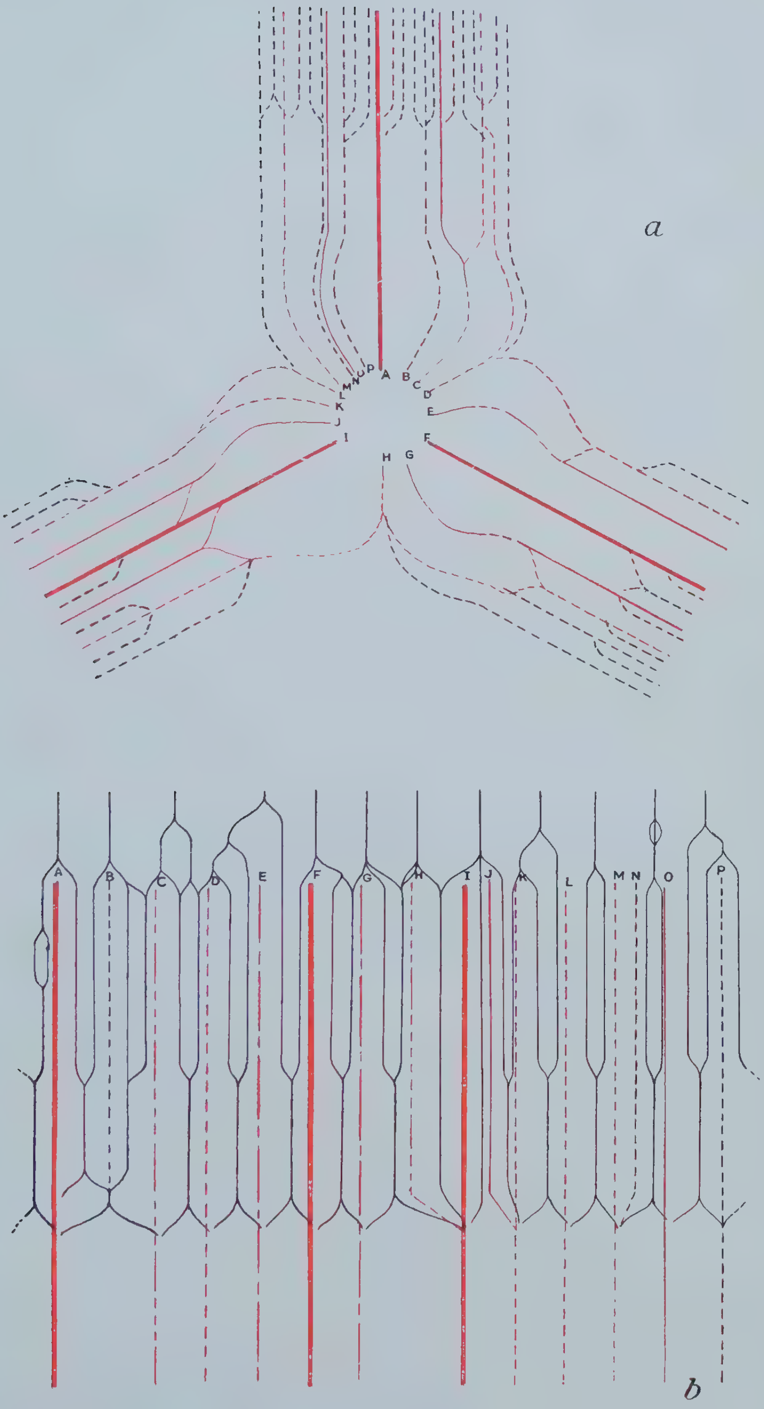

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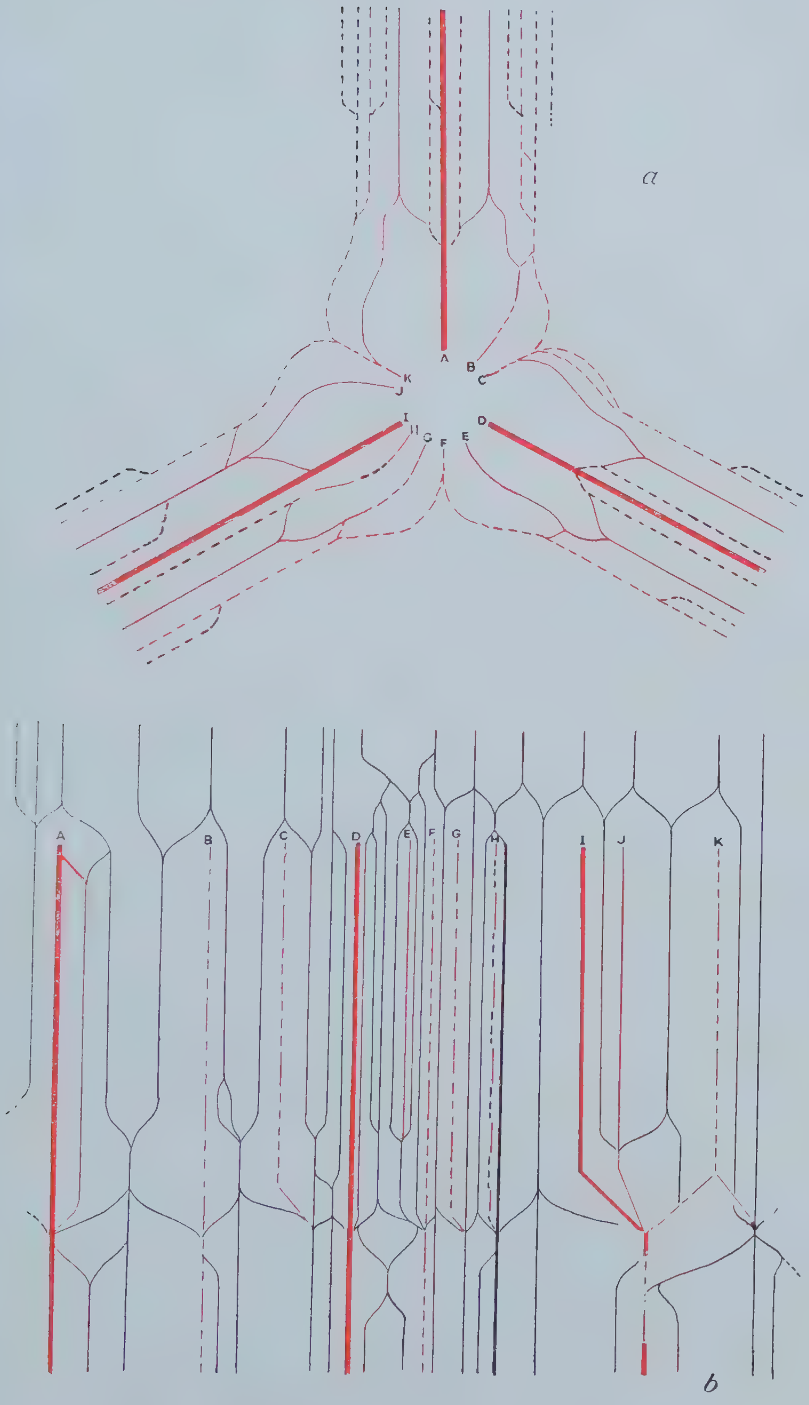

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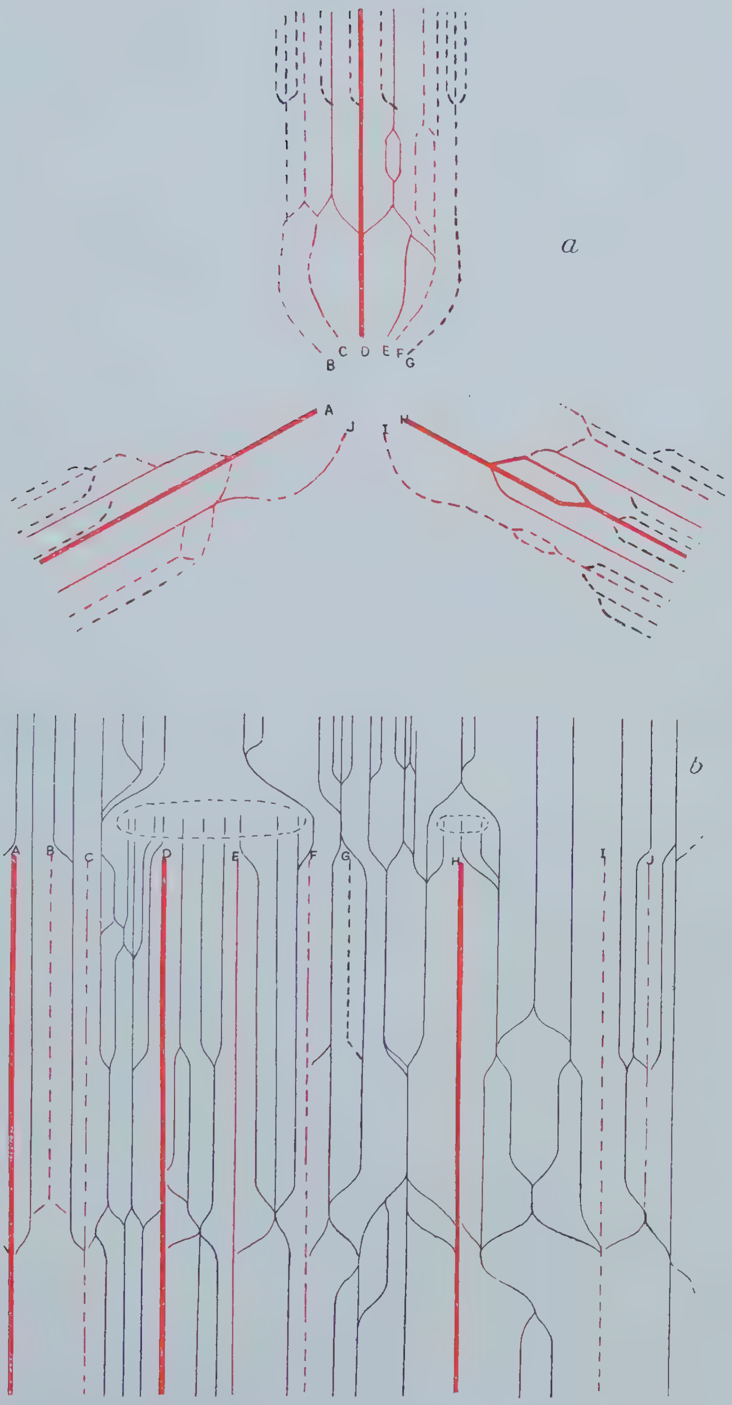

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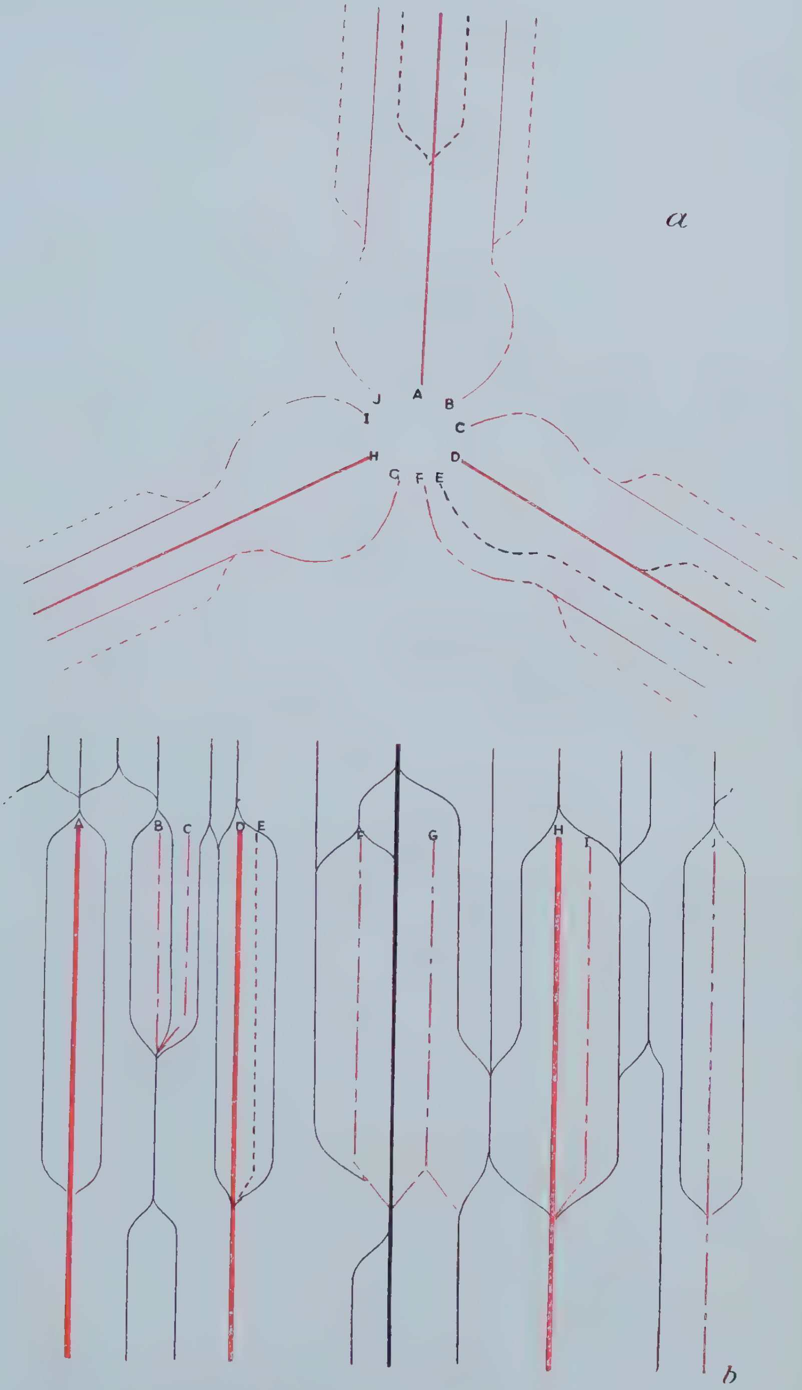

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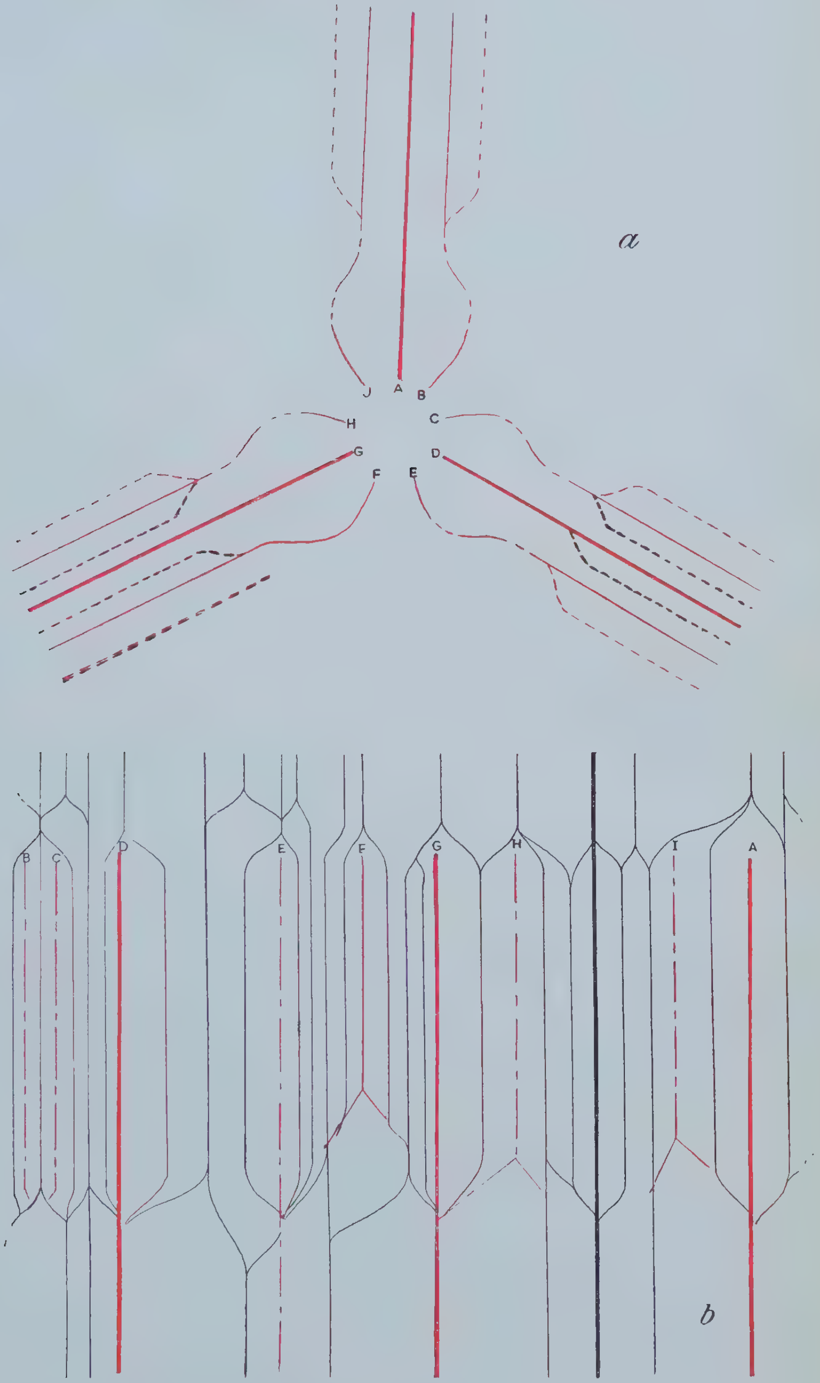

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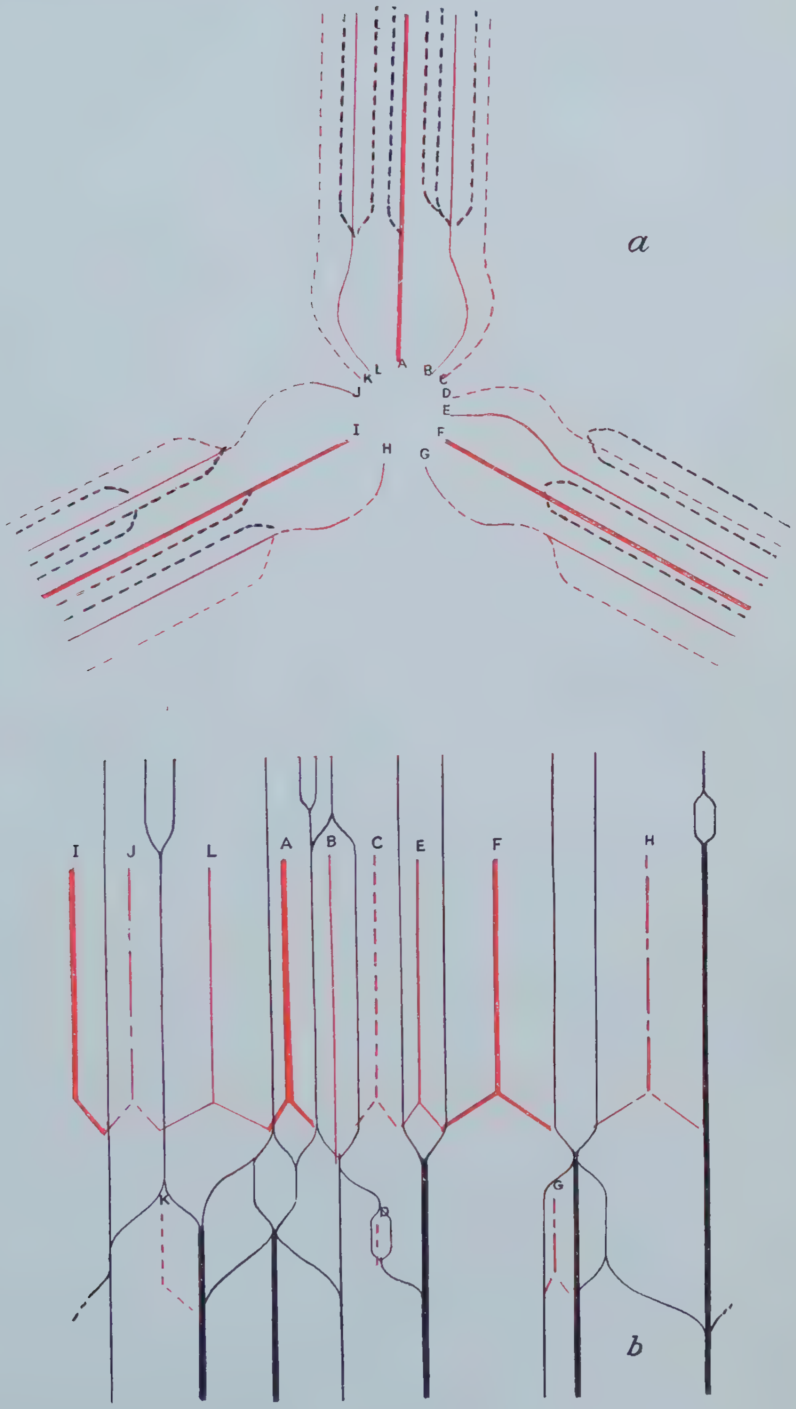
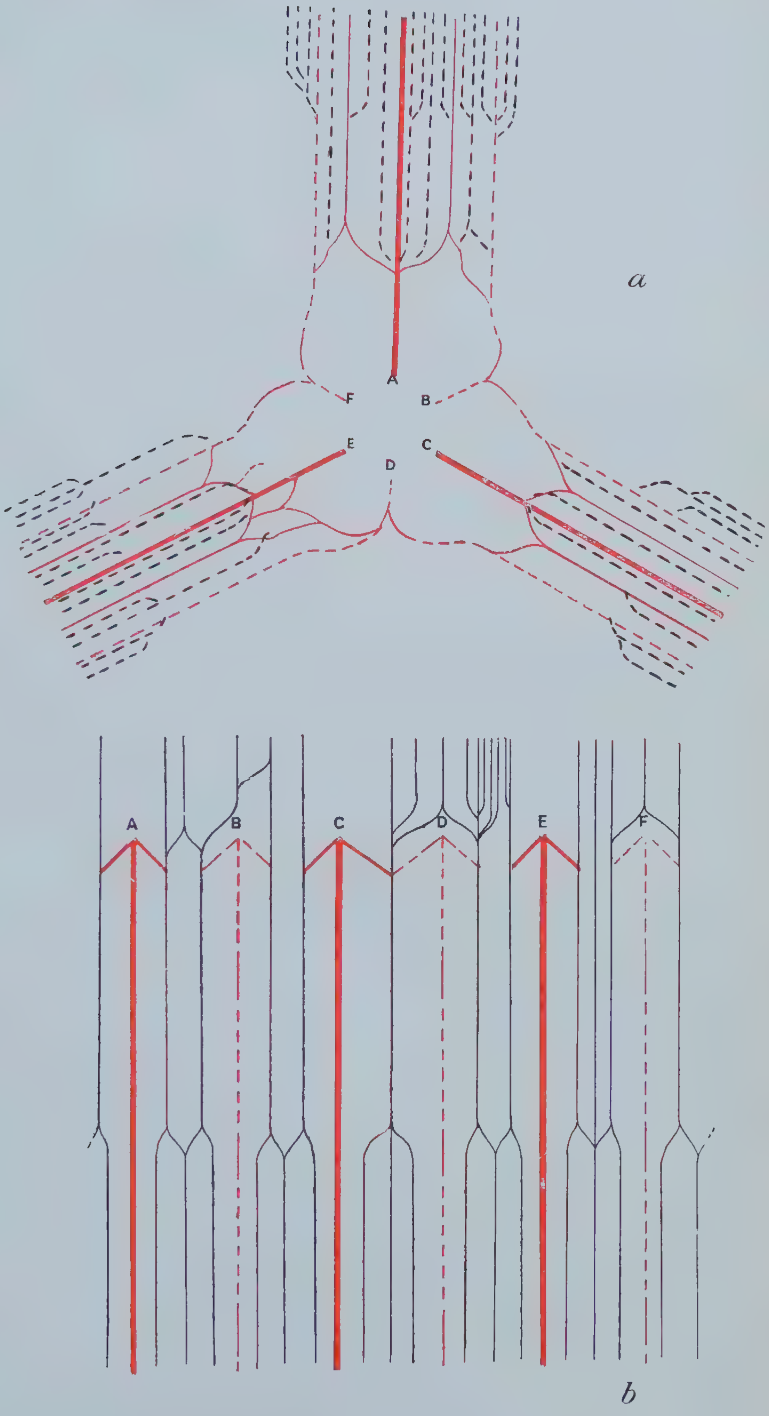


RANUNCULUS FICARIA.



ERANTHIS HYEMALIS.

# The Pimpinellas of Tropical Africa. By CECIL NORMAN, F.L.S.

[Read 6th January, 1926.]

THE following is an attempt to give a systematic account of the Pimpinellas of Tropical Africa. As in all Tropical African genera, the number of described species has largely increased in recent years. Five species were dealt with in the 'Flora of Tropical Africa' (1877)—thirty-one are considered here. I have had access to the material at the British Museum and at Kew, and, thanks to the kindness of Dr. A. B. Rendle, I have seen the types or authentic material from Berlin of species not in this country and unnamed material from Brussels. To all concerned I here tender my thanks. In spite of all, more specimens are much needed, some species being known from only one plant, some from only one gathering. Still, it is hoped that this paper will prove useful, if it is only by bringing together in one easily accessible place the species so far known, and thus enabling the future worker to avoid—or, at any rate, to beware of—some of the pitfalls that beset his path.

*Pimpinella* is a widely-spread Old World genus, occurring in Europe, Asia without the tropics or on elevated regions within, and in Africa and the neighbouring islands. There are perhaps some 150 species.

In Africa it occurs in the botanical regions, though very sparingly (as regards species) in North and South Africa—about four species in each. In the tropical region it occurs, or may do so, wherever the elevation ranges from about 3000 ft. to about 10,000 ft., provided there is sufficient rainfall. It is probably owing to its generally very low elevation that no species (so far as I know) has been found in the vast tract of land west of the Cameroons (excluding N. Nigeria), and owing to its generally high elevation that the rest of the tropical region is so rich in this essentially temperate genus.

It appears that the species, for the most part, are restricted in range, but there are several notable exceptions: e. g., *Pimpinella oreophila* occurs on the Cameroons Mts., Mt. Melangi (in Nyassaland), and on the mountains of Abyssinia; *P. Buchananii* in Nyassaland, Belgian Congo, and Angola, being probably the commonest Tropical African species. Only one species occurs in both Tropical and South Africa—viz., *P. caffra*. This plant, originally collected in Natal, occurs also on the mountains of Abyssinia, but nowhere in between, so far as is yet known—a most interesting example of interrupted distribution. Has the migration been from north to south or from south to north? (South Africa easily represents the southern limit of the genus.

In no other part of the world does it reach as far south as the tropic of Capricorn.)

No species are common to North and Tropical Africa.

All the Tropical African species, except two, belong to Drude's subgenus *Eu-pimpinella*. This he divides into the two sections: i. *Tragoselinum*, plants with glabrous ovary; ii. *Tragium*, plants with hairy ovary. As regards the second section, it should be remembered that the presence of hairiness is best determined in the early stages of growth, as in some species it tends to disappear as the plant matures. The sections are subdivided into (*a*) species with simple, (*b*) species with pinnate root-leaves.

Here it should be noted that many simple-leaved species often exhibit one or more trifoliate leaves mixed with the simple ones—probably all do so at times. Apparently it may be taken that trifoliate root-leaves indicate a simple-leaved species *, even if no simple leaf is found on a particular specimen. The pinnate-leaved plants, on the contrary, though showing much variation in the root-leaves, seem always to maintain the truly pinnate character. These remarks apply, of course, only to the plants under consideration.

## *Descriptive Key of the Species.*

Subgenus EU-PIMPINELLA Drude, in Pflanzenf. iii. pp. 8–196. Petals obcordate, with infolded apex white or reddish, rarely yellow; style as long as or usually much longer than the stylopodium, which is conical and free from the calyx. Bracts and bracteoles usually wanting. Fruit smooth and glabrous, or hairy.

I. Section *Tragoselinum* DC., Prod. iv. p. 199. Ovary glabrous.
  A. Radical leaves normally simple (see remarks above).
    i. Radical leaves suborbicular or subtriangular.
      „ „ ±5–6 cm. long and across the base; stem quite glabrous ........................ 1. *P. filiformis.*
      „ „ ±3–6 cm. long and 3–4 cm. across the base; stem densely pubescent .............. 3. *P. caffra.*
      „ „ ±2 cm. long and 1·5 across the base; whole plant quite glabrous ................ 2. *P. neglecta.*
      „ „ ±1 cm. long and across base; plant pubescent .............................. 4. *P. kilimandscharica.*
    ii. Radical leaves oblong-lanceolate ...................... 6. *P. trifurcata.*
    iii. Radical leaves usually siniform; teeth long, apiculate .... 7. *P. acutidentata.*
    iv. All lower leaves trifoliate .......................... 5. *P. kyimbilaensis.*
  B. Radical leaves pinnate.
    i. Pedicels thick and stout (at any rate in fruit).
      Leaflets orbicular (margins crenate) ........ ........ 11. *P. oreophila.*
      „ lanceolate or ovate-lanceolate; umbel rays up to 3 cm. ................................ 8. *P. Stolzii.*

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* *P. etbaica* seems a possible exception.

ii. Pedicels always hair-like.

Leaflets ovate-lanceolate, petiolate; umbel rays not above 1·5 cm. .................. 9. *P. Buchananii.*

„ broadly linear, subcordate, sessile .................. 10. *P. favifolia.*

„ ±orbicular (margins acutely dentate) .................. 12. *P. keniensis.*

C. Radical leaves pinnatisect .................. 13. *P. Hombléi.*

II. Section *Tragium* DC., *l. c.* Ovary hairy.

A. Radical leaves normally simple (see remarks above).

* Perennials or Biennials.

1. Umbel rays very many, exceeding 12 (except in *P. Ledermannii*), thick and upright; flowers very numerous, more than 20, with many males in each partial umbel.

*a.* Umbel rays glabrous, more than 12.

Radical leaves thick and fleshy .................. 14. *P. Gossweileri.*

„ „ thin; petioles glabrous or nearly so.

„ „ up to 14 cm. broad; base widely cordate .................. 15. *P. Mechowii.*

„ „ ±5 cm. broad; base truncate .................. 16. *P. robusta.*

Petioles densely pubescent.

Radical leaves: base cordate, with narrow sinus .... 17. *P. platyphylla.*

*b.* Umbel rays hairy.

Rays ±20 .................. 18. *P. Engleriana.*

Rays 7 or fewer .................. 19. *P. Ledermanii.*

2. Umbel rays few, less than 10 (except in *P. Volkensii*); flowers ±12 in each partial umbel, hermaphrodite.

*a.* Stem and rays glabrous.

i. Fruit with closely-appressed hairs.

Leaves and petiole quite glabrous .................. 22. *P. Volkensii.*

„ pubescent, especially the petioles .................. 20. *P. huillensis.*

ii. Fruit with spreading hairs .................. 21. *P. Welwitschii.*

*b.* Whole plant cinereo-pilose .................. 23. *P. Rivæ.*

** Annual, very slender, ±15 cm. high .................. 24. *P. tenuissima.*

B. Radical leaves pinnate.

Plant nearly glabrous, hairs on fruit appressed; leaflets closely toothed, thin .................. 25. *P. præventa.*

„ scabrid, hairs on fruit straight .................. 26. *P. peregrina.*

„ softly pilose, hairs on fruit hooked .................. 27. *P. camptotricha.*

„ nearly glabrous, hairs on fruit hooked, leaves pinnatisect. 28. *P. etbaica.*

„ pubescent, ovary sparsely hairy, leaflets ± deeply incised. 29. *P. nandensis.*

Subgenus Reutera (Boiss) B. & H., as subgenus in Gen. Pl. i. p. 894. Leaves pinnate, segments toothed or dissected; flowers yellow (or white in Trop. Afr. species). Fruits glabrous or papillose, bracts and bracteoles conspicuous in Trop. Afr. species.

Fruit minutely papillose .................. 30. *P. simensis.*

„ glabrous, smooth .................. 31. *P. imbricata.*

## PIMPINELLA Linn. Syst. ed. 1 (1735).

Benth. & Hook. f., Gen. Plant. i. p. 893.
Engler & Prantl, Pflanzenfam. iii. pp. 8–195.

### Subgenus EU-PIMPINELLA Drude.

Section I.—**Tragoselinum.** Fruit glabrous.

1. P. FILIFORMIS Wolff, in Feddé Rep. xvi. p. 237 (1919).

*P. pseudo-caffra* Norm. in Journ. Bot. lxi. p. 134 (1923).

Belgian Congo: in damp places, Kundelungu, *Kassner* 2783.

A distinct species, characterized by the tall slender terete stem and large leaves.

2. P. NEGLECTA Norman, sp. nov.

Planta humilis perennis, semi-procumbens, omnino glabra; radice elongata fusiforme sub-lignosa, *caule* ramoso, *foliis radicalibus* simplicibus, breviter petiolatis, oblongo-orbicularibus basi leviter cordatis, margine acute dentatis; *foliis caulinis* ad bracteas vaginantes reductis; *umbellis* magnis ±6 radiatis, radiis longis crassis æqualibus; *umbellulis* ±9 pedicellatis, pedicellis crassiusculis; involucro et involucello nullis; *petalis* flavis (ex coll.) apice inflexis; *ovario* glabro, stylopodio plano stylis brevissimis.

*Principal measurements.* Leaves ±2 cm. × 1·5 cm.; petioles about 2 cm. long; radii 2–3 cm. long.

*Hab.* Rhodesia: Mazoe District, alt. 4200 ft., September 1906, *Eyles* 404 in Herb. Mus. Brit. (type); "between Broken Hill zinc mine and Bwana Micuba copper mine," *C. E. F. Allen* in Herb. Kew, *sine no.*

A well-marked species, readily distinguished by the lax habit, long radii, "yellow flowers," acutely toothed leaf-margins, and in being completely glabrous. Apparently allied to the next following.

3. P. CAFFRA D. Dictr. Syn. Pl. ii. p. 947.

*Hab.* S. Abyssinia: between Haarar and Addis Ababba, *Capt. M. S. Wellby, s. n.* in Herb. Kew; also in Natal.

The whole plant is densely pubescent except the fruit, which sometimes has a few scattered hairs.

Capt. Wellby's plant is indistinguishable from plants from Natal and extreme east of Cape Colony. It appears to be the only known specimen from Abyssinia, but there is no evidence of any mistake, so the facts may be accepted, at least provisionally, as a most interesting case of interrupted distribution. At the same time confirmation is urgently desired.

4. P. KILIMANDSCHARICA Engler, in Bot. Jahrb. xix. Beibl. n. 47 (1894), p. 42.

*Hab.* Kilimanjaro: "3200–3400 metres in the Johannes Gorge and open grass-land above," *Volkens* 1196.

An erect plant of low stature with obtusely crenate leaf-margins and rather dense pubescence, especially on the radii and petioles.

5. P. KYIMBILAENSIS Wolff, in Feddé Rep. xxii. p. 348 (1926).

*Hab.* Kyimbila District, Tanganyika Territory, *Stolz* 2512 in Herb. Mus. Brit. and Kew.

There are no radical leaves preserved, but they are probably simple. Apparently allied to and certainly a good deal like *P. ebracteata* from Madagascar.

6. P. TRIFURCATA Wolff, *l. c.*

*Hab.* Kyimbila District, Tanganyika Territory, *Stolz* K. 14 in Herb. Mus. Brit. and Kew.

The root-leaves somewhat recall the stem-leaves of *P. Ledermannii* in shape and toothing, though the two are widely separated. There is much variation in shape and toothing of the leaflets of the stem-leaves.

7. P. ACUTIDENTATA Norman, sp. nov.

Herba tenuissima perennis circa 35 cm. alta, caule terete inferne sparsissime pubescente, superne glabro ; *foliis basalibus* nervis subtus pubescentibus, dense glabris, reniformibus, vel rarius subtriangularibus basi leviter excavatis, marginibus dentatis, dentibus longe apiculatis, inferne valde reticulatis, petiolo brevi omnino vaginante suffultis ; *foliis caulinis* paucissimis ad bracteas vaginantes reductis, vel nullis ; *umbellis* exinvolucratis magnis, ±5 radiatis, radiis inæqualibus patentibus ; *umbellulis* exinvolucellatis ±7 pedicellatis, pedicellis filiformibus, subæqualibus : petalis minutis, *stylis* longiusculis, *stylopodie* parvo sub-plano ; *fructu* pro genere magno, rotundato glabro.

*Principal measurements.* Reniform leaves to 5 × 6·5 cm. ; triangular leaves up to 6 × 5·5 cm. (across the base) ; petiole 2–3 cm. ; radii 3–6 cm. ; pedicels ±4 mm.

*Hab.* Belgian Congo : "Region du Lualaba, Katanga," *Homblé* 1006 (type) in Herb. Brux. ; Upper Katanga, *A. Hock*, *s. n.* ; Vallé de la petite Luemba, *A. Hock*, *s. n.*

Somewhat like *P. platyphylla*, but separated by the fruit. The leaves are remarkable for the long slender teeth. Of the five specimens seen, all have reniform leaves except one of the two plants on the type-sheet.

8. P. STOLZII Wolff, in Engler's Jahrb. lvii. p. 277 (1922).

*Hab.* Nyassaland : N. end of Lake Nyassa near Langenburg, 1000 m., *Stolz* 692. Belgian Congo : Elizabethville, *Bequaert* 297 in Herb. Brux.

Unfortunately I have seen no authentic material, the scrap at Kew being useless, but from the description I place Bequaert's specimen here. The larger leaves, and especially the much longer umbel rays, seem to me the true distinctions from *P. Buchananii*. I do not notice much thickening of the pedicels, referred to by Wolff.

9. P. Buchananii Wolff, in Engler's Jahrb. xlviii. p. 269 (1912), and Jahrb. lvii. p. 227 (1922).

Nyassaland, *Buchanan* 709; Mulinda Plateau, 900 m., *Stolz* 1449 *; Shire Highlands, Zambesia, *Buchanan* 268. A vigorous specimen with leaflets up to 7 cm. long.

Belgian Congo, *Kassner* 2478. This specimen is more hairy on the lower stem and petioles than any of the others; but this is easily accounted for by its being a much younger plant—it is not yet fully in flower; the leaflets exactly match *Stolz* 1449 in shape and toothing, but are somewhat larger.

Elizabethville, *Homblé* 203 in Herb. Brux.

10. P. favifolia Norman, in Journ. Bot. lxi. p. 133 (1923).

Belgian Congo: Kasenza River, Lake Mweru, *Kassner* 2818.

This, though perhaps allied to *P. Buchananii*, of which it has the hair-like pedicels and the fruit, is quite unlike any other *Pimpinella* I have seen. The leaves are very remarkable; unfortunately, they are badly pressed, and so difficult to describe. The leaflets are sessile, close together and subcordate, broadly linear or linear-lanceolate; apiculus and teeth horny. The plant is about 4 ft. high and certainly not an annual as originally suggested.

11. P. oreophila Hook f., in Journ. Linn. Soc. vii. p. 195; Hiern, in Flor. Trop. Afr. iii. p. 14 (1877).

*Hab.* Fernando Po, 9500 ft., *Mann*; Cameroon Mountains, 10,000 ft., *Mann*; Abyssinia, 10,000 ft., *Schimper* 1502.

A rigid plant with crenate margins to the leaflets.

There is a plant at Kew, *Adamson* 370, from Mount Melange (6–7000 ft.), with narrow incised leaflets which I take to be a form of *P. oreophila*. The upper stem leaves often show an approach to this form, if they are not sometimes identical with it.

The distribution is very remarkable.

12. P. keniensis Norman, sp. nov.

Herba perennis circa 23 cm. alta radice fusiforme, *caule* ramoso sparse pubescente, *foliis basalibus* pinnatis 2–3-jugatis petiolo piloso; foliolis suborbicularibus subtus præsertim sparse pubescentibus, sessilibus vel subsessilibus marginibus dentatis, dentibus acutis apiculatis, basi truncatis vel attenuatis, foliolo terminali lateralia vix superante; *foliis caulinis* ad bracteas vaginantes pinnatas reductis; *umbellis* ±6–8 radiatis, radiis tenuissimis, glabris; *pedicellis* tenuibus 6–9, *involucro* et involucellis nullis; *petalis* albis, *ovario* glabro, stylopodio plano, *stylis* brevibus.

*Principal measurements.* Leaf with petiole 4–6 cm.; leaflets ±1·5–2 cm. long and broad; umbel rays 1–1·5 cm.

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* Sent out from Berlin as *P. Engleriana*, but referred to *P. Buchananii* by Wolff in Engler's Jahrb. lvii. p. 228, no doubt rightly.

*Hab.* Kenya Colony, *Mrs. Prescott-Decie* (type); Hills about Kikuyu, *Scott-Elliott* 6739 Herb. Kew.

Allied to *P. oreophila*, but readily distinguished by the acutely-toothed margins of the leaves and the slender rays.

13. P. Hombléi Norman, sp. nov.

Herba perennis alta, circa 4 ped. alta, omnino glabra radice lignosa, caule striato inferne sulcato, leviter ramoso, *foliis basalibus* profundissime pinnatisectis, 3-jugatis segmentis longissimis, linearibus acutis ad ·8–1·4 cm. inter se remotis, marginibus remote acuteque serratis petiolo breviter vaginante, *foliis caulinis* similibus sed minoribus, *umbellis* exinvolucratis ±6 radiatis radiis inæqualibus patentibus, *umbellulis* exinvolucellatis ±10 pedicellatis pedicellis filiformibus æqualibus, floribus hermaphroditis, petalis minutis flavis (ex coll.), stylopodio sub-plano, stylis brevibus fructu (immaturo) glabro.

*Principal measurements.* Leaves, including petiole, up to 22 cm. long; leaf-segments up to 16 cm. long and ±·3–·6 cm. broad (the terminal segment longer than the upper pair); umbel rays 2–3·5 cm.; pedicels ·3–·5 cm.

*Hab.* Belgian Congo: "Vallée de Kapiri," Katanga, *Homblé* 1225.

This species is remarkable for the pinnatisect leaves, which in appearance somewhat recall *Cicuta* sp. The first is quite immature, but the plant has all the characters of *Eu-pimpinella.*

Section II.—**Tragium.** Ovary hairy.

14. P. Gossweileri Wolff, in Feddé Rep. xvi. p. 234 (1919).

Angola: N'Bango Malange, "in high grass skirting the Pandanus," *Gossweiler* 1267.

This species is remarkable for its thick fleshy leaves, peculiar serration, and the disagreeable smell of the whole plant (*Gossweiler*).

15. P. Mechowii (Engl.) Wolff, in Engler's Jahrb. lvii. p. 226 (1922).

*P. Welwitschii* Engl., var. *Mechowii* Engl. Hochgebirges Fl. p. 319 (1892).

Angola: Melange, *Mechow* 471 in Herb. Berol.

The root-leaves are larger than in any other African species and thin in texture. Wolff has rightly raised it to the rank of a species; the affinity is with *P. Gossweileri* and its allies, and not with *P. Welwitschii.*

16. P. robusta Norman, in Journ. Bot. lx. p. 119 (1922).

Angola: Cuanza norte District, between Angage and Camabatela, *Gossweiler* 7473.

Remarkable for the round stiff stem, and especially for the very large well-developed lower stem-leaves, all trifoliate with coarse sharp toothing. One of the largest species. The affinity is with the two preceding species, and not with *P. Welwitschii* as stated in the original description.

17. P. PLATYPHYLLA Welw. ex Hiern, Cat. Welw. Afr. Pl. i. p. 426 (1900).

*P. Welwitschii* Engl., var. *Buchneri* Engl., in Hochgebirges Fl. p. 319.

Angola: Pundo Andongo, *Welwitsch* 2504; Melange, *Buchner* 81 in Herb. Berol.

The stem-leaves are rather large, either almost orbicular or more often oblong-orbicular; the sinus at the base narrow and rather deep.

18. P. ENGLERIANA Wolff, nom. nov. in Herb. Berol.

*P. tomentosa* Engler (non Walz.), in Jahrb. xxx. p. 368 (1901).

*Hab.* Tanganyika Territory: Usagara, *Goetze* 1125 in Herb. Berol.

The densely cinereo-pilose umbel rays are the distinguishing feature.

19. P. LEDERMANNII Wolff, in Engler's Jahrb. xlviii. p. 270 (1912).

*P. Tessmannii* Wolff, in Feddé Rep. xvii. p. 170 (1921).

*Hab.* Cameroons: Markt Singwa, *Ledermann* 1620 (without root-leaves); Ngaundere, *Tessmann* 2711 (with root-leaves). Both in Herb. Berol.

Easily recognized by the short and few umbel rays (in all the allied species they are very many) and the narrow oblong lower stem-leaves.

Having seen the type-specimens of both *P. Ledermannii* and *P. Tessmannii*, it seems to me that they are one and the same species, Tessmann's specimen supplying the root-leaves that were missing in Ledermann's. The umbel rays in *P. Tessmannii* are rather more slender than in the other, but Tessmann's plant is in a younger state, which would account for this. The root-leaves of *P. Ledermannii* as here understood are much like those of *P. platyphylla.*

20. P. HUILLENSIS Welw. ex Engler, in Hochgebirge's Fl. p. 319 (1892).

*Hab.* Angola: Huilla, *Welwitsch* 2502.

This plant is remarkable for the very closely appressed hairs of the fruit. It was this character, I suppose, that caused Welwitsch to describe the fruit on his labels as "muriculate." Certainly the appearance of the fruit is unusual; the hairs are very deciduous, so that the ripe fruit is almost glabrous (except on the ribs), and the styles are remarkably short.

21. P. WELWITSCHII Engler, *l. c.*

*P. huillensis* Engl., var. *elatior* Welw. ex Hiern, Cat. Welw. Pl. i. p. 426.

Angola: Huilla, *Welwitsch* 2503, 2503 *b*; *Gossweiler* 3128 (no locality), 3177 (near Kutchi); *Wellman*, Bailundo District, Herb. Kew.

The hairs on the fruit of this species are thick and spreading, and though somewhat deciduous, much less so than in the last, and the styles are rather long. On these characters only it is here separated from *P. huillensis.*

22. P. Volkensii Engler, in Pflanzenw. Ost. Afr. C 299 (1895).

Kilimanjaro, 3200 m., *Volkens* 2025; "3rd day from Eldona Ravine," *Whyte* in Herb. Kew; Mt. Kenya, 6500 ft., *Battiscombe* 725 in Herb. Kew: a stouter plant showing many trifoliate leaves, presumably this species.

Usually a smaller and much more slender plant than any of its near allies.

23. P. Rivæ Engler, in Ann. Ist. Bot. Rom. vii. p. 22 (1898).

Somaliland: between Alghe and Oi, *Riva* 1237 (in Rome?).

No specimen seen.

24. P. tenuissima Norman, sp. nov.

Herba annua (ut videtur) humilis circa 15 cm. alta erecta, tenuis; caule, pubescente demum glabro, ramoso; foliis radicalibus simplicibus subtriangularibus basi profunde cordatis, marginibus leviter dentatis; foliis caulinis multinodis trifoliolatis, foliolis sessilibus vel sub-sessilibus marginibus dentatis (vel rarius integris) lateralibus sub-rhomboideis vel lanceolatis, terminalibus late vel anguste lanceolatis et lateralia semper excedentibus: umbellis 4–6 radiatis, radiis glabris valde inæqualibus, umbellulis 8–10 pedicellatis, pedicellis inæqualibus: involucro et involucello nullis; petalis albis apice inflexis, ovario pilis longis albidis obtecto; stylopodiis cericis conspicuis; stylis longis patentibus.

*Principal measurements.* Base-leaves 2 cm. × 1·5 (across the base); petiole ± 3 cm.; stem-leaves: terminal leaflets ± 1 × ·7 cm., lateral ± ·8 × ·5 cm.; radii ·5–1·5 cm.

Eritræa: Mont Bosco, près Saati, *Schweinfurth & Riva* 569 in Herb. Kew.

A pretty little plant, apparently related to *P. eriocarpa* from Syria and Mesopotamia.

25. P. præventa Norman, sp. nov.

Herba gracilis 1–3 ped. alta (ex coll.), *caule* ramoso terete glabro; *foliis basalibus* pinnatis, ambitu triangularibus 2- vel 3-jugatis, pinnis imis maximis, longiuscule petiolatis, petiolulis rachideque pubescentibus, ceteris sessilibus vel subsessilibus; laminis membranaceis, lanceolatis acuminatis basi truncatis vel leviter attenuatis, marginibus arcte acutissimeque serratis, superne glabris, inferne pilis rigidulis (nervis præsertim) sparse obtectis; terminali pinnis imis æquali. *Umbellis* exinvolucratis ± 7-radiatis, radiis tenuissimis patentibus subæqualibus demum glabris; *umbellulis* exinvolucellatis multipedicellatis pedicellis pubescentibus valde inæqualibus; *flores* hermaphroditi albi, *stylis* longissimis reflexis, *ovario* pilis valde adpressis obtecto.

*Measurements.* Radial leaves up to 13 cm. (including petiole); lowest leaflets 3 cm. × 1–1·5 cm.; topmost leaflets 2 cm. × 1 cm.; petiole, lowest leaflets ·7 cm.; umbel rays up to 2 cm.; pedicels up to 5 cm.

*Hab.* N. Nigeria: Vom, Bauchi Plateau, alt. 3000–4500 ft., *J. Dent Young* 107 in Herb. Kew.

A very distinct species, the thin delicate leaves being unlike any other in texture and toothing; moreover, it is so far the only Nigerian species.

26. P. PEREGRINA Linn. Mant. ii. p. 357.

*P. hirtella* A. Rich. Flor. Abyss. i. p. 323 (1847).

Abyssinia, *Schimper* 272, 6200 ft.; 355. Also in South Europe and Asia Minor.

The African specimens do not seem to differ in any way from those of Europe and Asia.

27. P. CAMPTOTRICHA Penzig, in Atti Congr. bot. Genova, (1893), p. 343.

Eritræa: Saganeiti, *Schweinfurth & Riva* 986 in Herb. Kew; "Hillsides, Erhruit," *Capt. H. Lynes*, R.N. (*sine no.*).

No authentic material has been seen, but the plants seem to agree with the original description. The lower parts are softly pilose, which is the obvious distinction from *P. peregrina*: in Admiral Lynes's plant the umbel rays are noticeably shorter than the plant from Saganeiti.

28. P. ETBAICA Schweinf., in Verh. Zool. Bot. Wien, ser. i. p. 667.

Nubia: Soturba hills, *Schweinfurth* 7474; Red Sea Province: Kamobrana, *MacDougal & Sykes* 86.

The leaves of this species are most variable, sometimes pinnately tripartite, sometimes trifoliate, with deeply-incised segments; sometimes the segments are linear.

29. P. NADENSIS Norman, sp. nov.

Herba perennis? pubescens vix ramosa, *caule* striato; *foliis* basalibus et caulinis (nisi supremis) consimilibus, pinnatis ±5 jugatis, foliolis ambitu sub-orbicularibus vel sub-triangularibus sessilibus, superioribus approximatis, imis ad 1·5 cm. remotis, margine profunde vel leviter incisis dentatis, utrinque pubescentibus, petiolo basi late vaginante (vagina ad 2 cm. longa). *Umbellis* exinvolucratis, magnis ±6 radiatis, radiis crassis densiuscule pubescentibus; *umbellulis* exinvolucellatis multipedicellatis, pedicellis crassiusculis, *petalis* albis, stylopodio subplano, *stylis* longiusculis, *ovario* sparse pubescente. *Fructus maturus ignotus.*

*Principal measurements.* Leaves with petiole up to 8 cm.; leaflets ±1·5×1 cm.; rays up to 3 cm.

*Hab.* Nandi, 7000–8000 ft., *Scott-Elliott* 6975 Herb. Mus. Brit. (type); Kilimanjaro, 3000–4000 ft., *Janssens* Herb. Brux.

This species can be readily distinguished from *P. keniensis*, which it more or less resembles by its thick and pubescent umbel rays as well as by the cutting of the leaflets, which is always variable. I suspect that the ripe fruit may prove glabrous, at least sometimes, as the ovary is only sparsely pubescent. It is probably an instance where the species might be placed under *Tragium* or *Tragoselinum* with equal propriety. The plant is further remarkable for the leafy stem, the stem-leaves being apparently identical with the root-leaves, which are badly preserved. Unfortunately, we have no collector's notes.

### Subgenus Reutera B. & H. f.

30. P. simense B. & H. f., Gen. Plant. i. p. 895; Hiern in Fl. Trop. Afr. iii. p. 14.

*Sium simense* Gay, in Rich. Fl. Abyss. i. p. 324.

*Hab.* Abyssinia, *Schimper* 266, 938, 1185; Kidung n'dogo, *Scott-Elliott* 6398 Herb. Kew. Kenya Colony; Aberdare Mts., *Sir James Evans*, Herb. Kew; fourth and fifth days' march from Eldona, *Whyte*, Herb. Kew.

Unlike any other Tropical African species, owing to the strong involucres and involucels, and papillose fruit.

31. P. imbricata (Schinz) Engler, in Kunene Sambesi Exp. p. 324 (1903), *Carum imbricatum* Schinz, *C. acanthophyllum* Welw.

*Hab.* Angola: Huilla, *Welwitsch* 2513; Angola, *Gossweiler* 3389, 3922, Katanga: Lualaba, *Homblé* 929 in Herb. Brux.

Related, as Engler points out, to *P. simensis*, and much like it, but with stiff prickly leaflets. The true position of these two plants is uncertain, and it is not without hesitation that I place them in the subgenus *Reutera*.

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### *Species doubtful or excluded.*

P. erythræ Armariæ in Ann. Ist. Bot. Roma, viii. p. 149.

No species seen. Does it differ from *P. Rivæ* Engl.?

P. Neumannii Engler (nomen), in Sitz. Preuss. Akad. Wiss. p. 734 (1906).

I have seen the specimen from Berlin (*Neumann* 133). It seems to be distinct, but the material is not good enough to describe.

P. ? Erlangeri Engler (nomen), *l. c.* p. 746.

I have also seen this from Berlin; it is not unlike a *Psammogeton*. The fruit is quite immature.

P. gymnosciadium Hiern, in Flor. Trop. Afr. iii. p. 14 (1877).

*Gymnosciadium pimpinelloides* Hochst., in Flor. xxvii. p. 20 (1844).

A study of the ample material at Kew makes it clear, I think, that this is a *Trachydium*, of which it has the typical and peculiar inflorescence; none of the fruit is really ripe, but it, too, seems typical. The plant should be called *Trachydium pimpinelloides* (nom. nov.). The affinity seems to be with some of the Indian or Chinese species rather than with *T. abyssinicum*, the only other African species. It is very much like the Himalayan *T. novemjugum*, but lacks the numerous bracteoles.

# Studies in the Phytoplankton of the Lowland Waters of Great Britain. No. V. The Phytoplankton of some Norfolk Broads. By BENJAMIN MILLARD GRIFFITHS, D.Sc., F.L.S.

(11 Text-figures.)

[Read 12th May, 1926.]

## INTRODUCTION.

BETWEEN Norwich and the sea there lies a large triangular area of low-lying land which in Roman times was a broad and shallow estuary. The estuary was originally formed in the period when the area now occupied by the North Sea was slowly submerged below tide-level. In Roman times, when the tide was out, the estuary presented the scene of wide mud-flats, through which wandered the rivers Bure, Yare, and Waveney. When the tide came in, the estuary became an expanse of water with a few very low islands emerging from beneath the surface. The tidal drift off the coast ran southwards, and the coastal detritus and the sediments brought down by the rivers were carried by the tidal drift, and formed a bar across the mouth of the estuary. In the course of the centuries the bar grew larger until it formed an almost complete barrier, and the river-silts tended more and more to be dropped on the floor of the estuary behind the barrier. The final result was to change the estuary into an area of very low marshy land, diversified with a few islands of slightly higher ground, and penetrated by slow-flowing rivers (see Marr, **16**, p. 165). The barrier formed the site upon which Yarmouth now stands. The old levels were not greatly affected by the changes, and the fall from Norwich to the sea is still only about two inches (Pallis, **17**, p. 218). The tide-water does not now come into the estuary because the great barrier at the mouth leaves only a very narrow channel at Yarmouth, and the sea-water flows in at flood-tide so slowly that the ebb occurs before the sea-water has come far inland. It is only when there is an exceptionally high tide and an on-shore wind that the tide can be held up sufficiently long to ensure penetration. On these occasions the heavy salt water creeps up under the lighter fresh water and causes a kind of underflooding which may do great damage to freshwater fish.

The silting of the area and its conversion into fen was not complete. In many places there were slightly deeper hollows in the original mud-flats, where the depth of water was too great to allow the invading marsh vegetation to obtain a footing. These areas therefore remained as open stretches of fresh water, while the shallower areas became gradually filled up with vegetation, and their levels were slowly raised by the accumulation of vegetable detritus *in situ*. The areas of open water constitute the Broads.

There are some sixty of them, varying in depth from fifteen to thirty feet*, and in area from one to twelve hundred acres. Many, but not all, are tidal waters in the sense that the tidal ebb and flow is perceptible, but not in the sense of being actually invaded by the sea-water. The tide comes in at Yarmouth and changes the outfall level, and the river-water accumulates for a time and the levels of the river and Broads are also raised temporarily. The rise and fall amounts to two feet or more at Brundall, just below Norwich. (For general account of the Broads, see Pallis, **17**, pp. 214–222.)

The result of this geographical evolution is that the various Broads have different ecological histories and are differing habitats at the present day. In August 1924 the writer examined the phytoplankton of the following places in the area :—

Group A. Wroxham Area : River Bure at Wroxham Bridge ; Wroxham Broad; River Bure below Wroxham Broad; a small broad immediately above Salhouse Broad, referred to in the text as "Upper Salhouse Broad."

Group B. Norwich Area : Surlingham Broad ; River Yare at Brundall ; Rockland Broad.

Group C. Yarmouth Area : Ormesby Broad.

The collection was made by towing behind a rowing-boat a conical net of 0·05 mm. mesh bolting silk. The collections were preserved on the spot with 2 per cent. formalin. The choice of Broads was determined by considerations of accessibility. Many of the Broads can be reached conveniently only by sailing-boat or motor-boat. The results of this brief sampling of the area show that a more extended survey would undoubtedly yield a rich harvest of algæ, particularly of Protococcales.

## TOPOGRAPHY AND PHYTOPLANKTON †.

### GROUP A.—**The Wroxham Area.**

River Bure at Wroxham Bridge.

The collection was taken just above the bridge at Wroxham. At this point the banks are bounded by wharves. Just above the point of collection there is a small and weedy broad between the main road and the railway. The plankton contained much muddy detritus stirred up from the bottom by river traffic, and also some amount of vegetable detritus. There were numerous dead and empty specimens of *Surirella*, *Gyrosigma*, *Campylodiscus*, and *Cymatopleura* from the muddy bottom of the river (see similar case at Burwell Lode, Upwear, Cambs, Griffiths, **11**, p. 120). The living material comprised :—cc. *Melosira varians, Pediastrum Boryanum*; c. *Fragilaria capucina*; r. *Pediastrun duplex*; rr. *Gomphosphæria lacustris, Scenedesmus quadricauda, Dictyosphærium pulchellum*; rrr. *Asterionella formosa, Pediastrum biradiatum.*

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* See also Hinton, **14**, p. 139. Local information in 1924 gives rather lower limits of depth.

† Frequency is indicated as follows:—ccc.=abundant, cc.=common, c.=fairly common, r.=a few, rr.=rare, rrr.=very rare.

### Wroxham Broad.

The Broad lies beside the River Bure some distance below Wroxham Bridge. It is connected with the river by channels at both ends. Its area is about one hundred acres, and it differs from other Broads in being some twenty feet in depth. As the surface is very little above sea-level, the bottom must be below sea-level in places. On rare occasions the Broad is underflooded with salt water. There is an extensive and sharply-defined fringe of *Arundo* around the Broad, and the slope of the sides is fairly steep. Some *Typha angustifolia* occurs on the north side, together with occasional *Scirpus lacustris*. The phytoplankton was very abundant and the water was brown in colour.

The plankton comprised :—ccc. *Melosira distans*; cc. *M. granulata*; c. *Fragilaria Crotonensis, Gomphosphæria lacustris, Cœlastrum sphæricum, Dinobryon stipitatum*; r. *Microcystis Holsatica, Chroococcus limneticus, Scenedesmus acuminatus, S. quadricauda*; rr. *Gloeotilia protogenita, Pandorina Moruṁ, Pediastrum Boryanum, Scenedesmus bijugatus* var. *alternans, S. opoliensis* var. *carinatus, Dictyosphærium pulchellum, Staurastrum tetracerum*; rrr. *Melosira varians, Asterionella formosa, Pediastrum duplex, P. Tetras, Chodatella Droescheri, C. longiseta, Scenedesmus denticulatus, S. Raciborskii, Ankistrodesmus falcatus* var. *mirabilis, Tetraedon minimum, T. caudatum* var. *incisum, Kirchneriella gracillima, Staurastrum paradoxum* var. *biradiatum.*

### River Bure below Wroxham Broad.

The collection in this reach of the river yielded a plankton which was totally different from that obtained in the river at Wroxham Bridge. The plankton was extremely abundant, and consisted mostly of the species dominant in Wroxham Broad. The plankton comprised :—ccc. *Melosira distans*; cc. *M. granulata*; r. *Fragilaria Crotonensis, Cœlastrum sphæricum*; rr. *Surirella* (empty); rrr. *Campylodiscus* (empty); *Pediastrum Boryanum, P. duplex, Scenedesmus opoliensis* var. *carinatus, S. quadricauda.*

### "Upper Salhouse Broad."

This little Broad immediately adjoins the river. It is two or three acres in area, more or less rounded in form, and has an abundant macroflora of water lilies and pond weeds round its sides. The plankton was abundant, and closely resembled that of Wroxham Broad. It comprised :—ccc. *Melosira distans*; cc. *M. granulata*; c. *Gomphosphæria lacustris*; r. *Microcystis*

*Holsatica*, *Chroococcus limneticus*, *Gloeotilia protogenita*, *Dictyosphærium pulchellum*, *Richteriella botryoides* var. *tetraedrica* ; rr. *Scenedesmus quadricauda*; rrr. *Surirella* (empty), *Pandorina Morum*, *Pediastrum Boryanum*, *P. duplex*, *P. duplex* var. *rugulosum*, *Cœlastrum sphæricum*, *Richteriella quadriseta*, *Chodatella Droescheri*, *Scenedesmus Hystrix*, *S. obliquus*, *S. opoliensis* var. *carinatus*, *S. Raciborskii*, *Tetraedron caudatum* var. *ncisum.*

## GROUP B.—**Norwich Area.**

### Surlingham Broad.

The Broad lies a short distance down the river Yare from Norwich, and is connected with the river by channels at both ends. Its area is about thirty acres, and the depth is not much over three or four feet. The surface of the Broad is spread with large islands of *Myriophyllum*, among the floating fronds of which are abundant masses of *Lemna gibba*, *L. polyrhiza*, and *L. minor*. A little *Hydrocharis* was also seen. The sides of the Broad are fringed with *Arundo.* The channels leading from the river to the Broad, and the banks of the river itself, have a fringe of *Poa aquatica* as well as the *Arundo.* There is a tidal rise of a foot or more in the river. The river is reported to go blue in summer, but not the Broad itself.

The phytoplankton of the Broad consisted largely of vegetable detritus and epiphytic organisms from the submerged macrophyta. The following were noted :—cc. *Nitzschia acicularis;* c. *Cyclotella operculata*, *Synedra Ulna* ; r. *Melosira varians*, *Fragilaria capucina*, *Oscillatoria chalybea* ; rr. *Actinastrum Hantzschii* ; rrr. *Pediastrum Boryanum*, *Scenedesmus quadricauda*, *Richteriella botryoides* var. *tetraedrica.*

### River Yare at Brundall.

The collection was taken from the reach which runs parallel to the Broad. The collection contained much muddy detritus. The organisms which were present were very similar to those in the Broad, but in different proportions :—c. *Nitzschia acicularis*, *Oscillatoria chalybea* ; r. *Melosira varians*, *Synedra Ulna* ; rr. *Cyclotella operculata*, *Actinastrum Hantzschii*, *Scenedesmus quadricauda* ; rrr. *Pediastrum Boryanum*, *Richteriella botryoides* var. *tetraedrica.*

### Rockland Broad.

The Broad lies some distance down the river from Surlingham. It lies immediately at the foot of high ground at Rockland St. Mary. It is a headwater, and is connected with the river by a single outlet channel about three-quarters of a mile long. The area of the Broad is about a hundred acres and the depth some six or seven feet. The sides are fringed with *Arundo* and *Typha angustifolia*, with smaller amounts of *Scirpus lacustris* and *Sparganium.* Well out in the Broad are several small islands of *Arundo.* The bottom has large patches of *Potamogeton* sp., and the bays are full of

*Nuphar*, *Hippuris*, and *Sagittaria*. The water-level changes with the tide. It is reported locally that a few years ago the Broad was under-flooded with salt water and the fish were killed. The plankton contained much flocculent vegetable detritus, together with :—ccc. *Cyclotella operculata* ; cc. *Dictyosphærium pulchellum*, *Tetrastrum apiculatum* (*Crucigenia apiculata*) ; c. *Asterionella formosa*, *Pandorina Morum*, *Dinobryon Sertularia* ; r. *Melosira varians* ; rr. *Pediastrum Boryanum*, *Scenedesmus quadricauda*, *S. obliquus*, *S. opoliensis* var. *carinatus* ; rrr. *Melosira granulata*, *Pediastrum duplex*, *Tetrastrum staurogenieforme*, *T. Rocklandensis*, sp. nov., *Lagerheimia Wratislaviensis*, *Actinastrum Hantzschii*, *Scenedesmus acuminatus*, *Richteriella botryoides* var. *tetraedrica*.

### Ormesby Broad, near Yarmouth.

This Broad is the northern end of a large and much branched sheet of water which is called Rollesby Broad in its central part and Filby Broad at its southern end. The three sections are defined by two main roads which cross the Broad at narrow points where there are embankments and bridges. The whole Broad is a headwater, and is drained to the river by the Muck Fleet at the southern end. The formation of the Broad was probably different from that of the other (Pallis, **17**, p. 220). The Broad is not tidal. At the time of collection, Ormesby Broad had a well-marked water-bloom of a blue-green colour. This is apparently normal for the season. The Broad was formerly used as a water-supply and, according to local information, "the water had to be filtered twice." The area is about two hundred acres, and the depth from six to ten feet. Around the margin there is a sharply-defined fringe of *Arundo* with fairly large patches of *Typha angustifolia* and small masses of *Scirpus lacustris*. Behind the rush-fringe on the north-east and north sides there is a wood of *Alnus* and *Pinus sylvestris*. The plankton was abundant and comprised :—cc. *Melosira granulata* ; c. *M. distans*, *Asterionella formosa*, *Anabæna spiroides*, *A. affinis*, *Aphanizomenon Flos-aquæ*, *Gomphosphæria lacustris*, *Microcystis æruginosa*, *Pandorina Morum*, *Pediastrum Boryanum*, *P. duplex*, *P. biradiatum*, *Dictyosphærium pulchellum* ; r. *Microcystis Flos-aquæ*, *M. Holsatica*, *Chroococcus limneticus*, *Pediastrum Boryanum* var. *longicorne*, *Scenedesmus acuminatus*, *Staurastrum dejectum* ; rr. *Gomphosphæria Naegliana*, *Pediastrum duplex* var. *clathratum*, *P. Kawraiskii*, *Tetraedron limneticum*, *Staurastrum tetracerum*, *Ceratium hirundinella* (two horned at base), *Diplopsalis acuta* ; rrr. *Anabœna circinalis*, *A. Lemmermanni*, *Pediastrum duplex* var. *rugulosum*, *P. Tetras*, *Cœlastrum sphæricum*, *Scenedesmus opoliensis* (?), *S. opoliensis* var. *carinatus*, *S. Raciborskii*, *Selastrum Bibraianum*, *Richteriella botryoides* var. *tetraedrica*, *Staurastrum paradoxum*.

The relative abundance of species and varieties of *Pediastrum*, as seen by counting five microscopic fields, was :—*Pediastrum Boryanum* 14, *P. Boryanum* var. *longicorne* 8, *P. duplex* var. *rugulosum* 0, *P. duplex* var. *clathratum* 3, *P. duplex* 12, *P. Kawraiskii* 4, *P. biradiatum* 15. Total 56.

## THE DISTRIBUTION OF THE ALGA-FLORA.

The uniformity in the general level of the district, the frequent presence of both upper and lower connecting channels between Broad and river, and the secondary tidal rise and fall of the fresh water, unite to bring about an association between river and lake which is not met with in other parts of the English Lowland area. In this district there is a marked tendency towards the intermingling of the moving-water habitat (kinetohydric) and the still-water habitat (statohydric), with a corresponding fusion between the respective potamo- and lacuplankton *. The following table of the stations from which collections were taken shows the relation of the two habitats :—

River Channels : River Bure above Wroxham Bridge ; River Bure below Wroxham Broad ; River Yare at Brundall.

Broads connected with the river by both upper and lower channels :
(*a*) Shallow : Surlingham Broad.
(*b*) Deep : Wroxham Broad ; "Upper Salhouse Broad."

Broads which are headwaters :
(*a*) Shallow and tidal : Rockland Broad.
(*b*) Deep and non-tidal : Ormesby Broad.

If the volume of the basin of the Broad is small in relation to the volume of river-water which flows into or through the Broad, the effect of the river-water will be proportionately greater than if the basin of the Broad was of greater volume—*e. g.*, Surlingham and Wroxham. Even in headwaters which are connected with the river by single channels only, the tidal rise and fall may cause river-water to flow into the Broad—*e. g.*, Rockland Broad. Ormesby Broad is without any tidal rise or fall, and the river effect, therefore, will probably be at its minimum.

The ecological meaning of the term "river" is obscure. Some of the chief features of rivers are given by Clark (4, p. 60 *seq.*). He says that a river, from the point of view of the chemical composition of its water, is the average of all the tributaries, plus rain- and ground-water. The smaller streams may be variable because of local conditions, but the larger rivers tend to resemble one another very closely, especially in their lower courses. The flowing river is well supplied with carbon dioxide from the air and from the decaying vegetation. Its salts are abundant, and they are kept in solution by the carbon dioxide. Precipitation is rare.

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* There is no term to denote the plankton of still water in general. The term *lacuplankton* is suggested (lacus, lacus=pool, lake, basin of a fountain ; Lewis and Short, Latin Dictionary, Oxford, 1880). The writer has shown (Griffiths, **10**) that the still-water plankton can be divided into the *limno-plankton* of the larger and deeper waters, the *bentho-plankton* of shallow waters, and the *heleo-plankton* of mixed or intermediate conditions.

It must, however, be pointed out that the rivers are of two distinct kinds. In the first group are those rivers in which the volume of water supplied by the tributaries is greater than the volume of water which the main channel will hold. Here the water of the main channel is being constantly changed by the flow of the stream. This is the type of river to which reference is made above.

In the second group are those rivers which, owing to accidents of geological development, have beds which are too large for their present drainage-areas, with the result that the volume of the main channel is greater than the volume of water supplied by the tributaries. Such rivers resemble greatly elongated lakes. The water in the main channel is not continually changed, but is like a long lake with a relatively small stream running through. Rivers of this kind are really statohydric habitats, and are only pseudo-kinetohydric. They may, in fact, develop typical limnoplankton of Myxophyceæ, *Ceratium hirundella* and *Asterionella.* Ecologically therefore, a river may be a very variable habitat, and may vary in type from one part of its course to another.

The Rivers Yare and Bure in this district are lower courses, and they may be considered as showing the features which Clarke describes—namely, a great abundance of dissolved salts held in solution to a large extent by the plentiful dissolved carbon dioxide. They may be considered as eu-kinetohydric habitats.

This habitat is apparently very unfavourable for most limnoplanktonts, but a few benthoplanktonts from the shallower weedy waters of the drainage area seem able to survive and form the so-called potamoplankton. Apart from casuals which have been swept into the stream by rainfall, there may be distinguished two types of potamoplanktonts—namely, (*a*) those which are as plentiful in the river as in the statohydric habitat, and (*b*) those which are more plentiful. In this area the former class is represented by *Cyclotella operculata* and *Actinastrum Hantzschii*, both of which are commonly found in rivers (see West, **25**, p. 445), and perhaps there might be added *Richteriella botryoides, Tetrastrum apiculatum*, and *Scenedesmus opliensis* var. *carinatus.*

The class which is more plentiful in the river than elsewhere may be represented by *Melosira varians*, which does definitely appear to be associated with weedy habitats through which run considerable volumes of water (see Griffiths, **6**, p. 426). Butcher (**3**), in his investigation of the plankton of the River Wharfe, Yorks, describes what is perhaps a parallel in *Gonatozygon monotœnium*, which is more plentiful in the river than in the still-water habitats. The rest of the wharf plankton appears to be more or less casual in type.

The chemical effect of the river-water upon the water of the statohydric Broad will be to increase the salts-content of that habitat. Pearsall (**19**) has pointed out the great influence of dissolved salts upon the periodicity of diatoms. As far as my experience goes, diatom abundance is also associated with considerable volume and depth of water, and high salts-content alone does not ensure diatom abundance. Shallow and weedy waters may show very high salts-content, but, nevertheless, there is no diatom abundance—*e. g.*, Ryton Willows Pool, co. Durham, and most small lowland pools (see Drew, **5**). With this proviso, Pearsall's explanation may be applied to account for the immense abundance of *Melosira granulata* and *M. distans* in Wroxham and Ormesby Broads. This dominance is not found in the River Bure above Wroxham Broad, but only in the Broad itself and in the river below, nor is it found in the shallow Rockland Broad. One might conclude that the significant ecological factors in this area are, first, a definitely limnoplanktonic habitat (*i. e.*, basins of some size and depth), and, secondly, the enrichment of the water of the basin by the infusion of river-water, which contains much dissolved salts. The same explanation of the enrichment of limnoplanktonic habitats by the salts brought in by rivers may also account for similar dominance of *Melosira* in the Danish and North German waters described by Wesenberg-Lund (**23**).

The River Yare at Brundall might be considered to have a potamoplankton in the sense given above. Its constituents are for the most part derived from the adjacent Surlingham Broad. *Oscillatoria chalybea*, however, is more plentiful in the river than in the Broad, and may therefore be considered as having its origin in the river. The latter is contaminated with town effluent.

The plankton of the River Bure is also derived from still-water habitats, with the addition of the empty tests of diatoms from the mud. Below Wroxham Broad the river swarms with *Melosira granulata* and *M. distans* from the Broad.

Wroxham Broad itself, and also "Upper Salhouse Broad," is mainly limnoplanktonic, but greatly affected by the influence of the water of the river. There is a marked absence of Myxophyceæ, *Asterionella* is rare, and the typical limnoplanktont of lowland waters, *Ceratium hirundinella*, was not found.

Rockland Broad, off the River Yare, is mainly benthoplanktonic or heleoplanktonic, but the presence of certain Protococcales indicates potamic influence.

Ormesby Broad is almost entirely limnoplanktonic. Myxophyceæ are abundant, *Asterionella* occurs in fair numbers and *Ceratium hirundinella* is also present. River-water influence is seen in the abundant occurrence of

*Melosira granulata* and *M. distans*. A peculiar feature of the plankton is the occurrence of several species of *Pediastrum* in considerable numbers. The presence of *Anabæna affinis* and *Diplopsalis acuta* point to relation with Continental waters rather than with other waters of the English Lowlands.

### *Relation to other Areas.*

The plankton found in this area differs rather markedly in character from that encountered in other parts of the English Lowlands. Geographically, the area is not paralleled elsewhere in Great Britain, and it is necessary to turn to the Continent to find a similar district. In Denmark, perhaps, one finds the closest parallel to the conditions prevalent in this Norfolk area, and the plankton of the Danish lakes correspondingly resembles that found here. The other lakes of the English Lowland area are for the most part rather deeper in proportion to their surface area, and their characteristic alga-floral dominants are Myxophyceæ, *Asterionella* and *Ceratium hirundinella*. *Melosira granulata* only occasionally occurs, as in Hanmer Mere and in White and Chapel Meres in the Shropshire-Cheshire district (Griffith, **8**, p. 92), and also in Upper Bittell Reservoir, near Bromsgrove, Worcestershire, but never in great abundance. The lake which most closely resembles the Broads in basin contour and depth is Hornsea Mere, E. Yorkshire, but this lake has a dominant Myxophycean flora together with a variety of *Ceratium hirundinella*. The significant geographical difference between Hornsea Mere and the Broads is the absence of river influence in the former, and this difference is shared by the other Lowland waters. It may be concluded, therefore, that the influx of river-water is the factor which differentiates this area from the rest of the Lowlands and equates it to the Danish area.

A peculiar feature of the Norfolk plankton is the absence of *Eudorina*. This alga has an extremely wide habitat range, and occurs in both neutral and alkaline waters and in all sizes of pools and lakes, and in very varied concentrations of dissolved salts. *Pandorina* is more restricted in occurrence, but, nevertheless, the influence of river conditions seems to favour it, and it is a characteristic "potamoplanktont." *Eudorina*, however, appears to find the influx of river-water unfavourable to its growth, and its absence from the plankton of the district is quite striking.

*List of Plankton Alga-flora.*

| | River Bure above Wroxham Broad. | Wroxham Broad. | River Bure below Wroxham Broad. | "Upper Salhouse Broad." | Surlingham Broad. | River Yare at Brundall. | Rockland Broad. | Ormesby Broad. |
|---|---|---|---|---|---|---|---|---|
| BACILLARIEÆ. | | | | | | | | |
| *Cyclotella operculata* Kuetz. | .. | .. | .. | .. | c | rr | ccc | |
| *Melosira varians* Ag. | cc | rrr | .. | .. | r | r | r | |
| ,, *granulata* Ehrenb. | .. | cc | cc | cc | .. | .. | rrr | cc |
| ,, *distans* Kuetz. | .. | ccc | ccc | ccc | .. | .. | .. | c |
| *Fragilaria capucina* Desmaz. | r | .. | .. | .. | r | | | |
| ,, *Crotonensis* Kitton | .. | c | r | | | | | |
| *Synedra Ulna* Ehrenb. | .. | .. | .. | .. | c | r | | |
| *Asterionella formosa* Hass. | rrr | rrr | .. | .. | .. | .. | c | c |
| *Nitzschia acicularis* Kuetz. | .. | .. | .. | .. | cc | c | | |
| *Surirella* sp. | c | .. | rr | rrr | | | | |
| *Cymatopleura* sp. | c | | | | | | | |
| *Campylodiscus* sp. | c | .. | rrr | | | | | |
| *Gyrosigma* sp. | c | | | | | | | |
| MYXOPHYCEÆ. | | | | | | | | |
| *Anabæna circinalis* (Kuetz.) Hansg. | .. | .. | .. | .. | .. | .. | .. | rrr |
| ,, *Lemmermanni* P. Richter | .. | .. | .. | .. | .. | .. | .. | rrr |
| ,, *spiroides* Kleb. | .. | .. | .. | .. | .. | .. | .. | c |
| ,, *affinis* Lemm. | .. | .. | .. | .. | .. | .. | .. | c |
| *Oscillatoria chalybea* Mertens | .. | .. | .. | .. | r | c | | |
| *Aphanizomenon Flos-aquæ* (L.) Ralfs | .. | .. | .. | .. | .. | .. | .. | c |
| *Gomphosphæria lacustris* Chod. | rr | c | .. | c | .. | .. | .. | c |
| ,, *Naegeliana* (Unger) Lemm. | .. | .. | .. | .. | .. | .. | .. | rr |
| *Microcystis æruginosa* Kuetz. | .. | .. | .. | .. | .. | .. | .. | c |
| *Microcystis Flos-aquæ* (Wittr.) Kirch. | .. | .. | .. | .. | .. | .. | .. | r |
| ,, *Holsatica* Lemm. | .. | r | .. | r | .. | .. | .. | r |
| *Chroococcus limneticus* Lemm. | .. | r | .. | r | .. | .. | .. | r |
| CHLOROPHYCEÆ. | | | | | | | | |
| ULOTRICHALES. | | | | | | | | |
| *Gloetilia protogenita* Kuetz. | .. | rr | .. | r | | | | |
| PROTOCOCCALES. | | | | | | | | |
| *Pandorina Morum* (Muell.) Bory. | .. | rr | .. | rrr | .. | .. | c | c |
| *Pediastrum Boryanum* (Turp.) Menegh. | cc | rr | rrr | rrr | rrr | rrr | rr | c |
| ,, ,, var. *longicorne* Reinsch | .. | .. | .. | .. | .. | .. | .. | r |
| ,, *duplex* Meyen | r | rrr | rrr | rrr | .. | .. | rrr | c |
| ,, ,, var. *rugulosum* Racib. | .. | .. | .. | rrr | .. | .. | .. | rrr |
| ,, ,, var. *clathratum* A. Br. | .. | .. | .. | .. | .. | .. | .. | rr |
| ,, *biradiatum* Meyen | rrr | .. | .. | .. | .. | .. | .. | c |
| ,, *Tetras* (Ehrenb.) Ralfs | . | rrr | .. | .. | .. | .. | .. | rrr |
| ,, *Kawraiskyi* Schmidle | .. | .. | .. | .. | .. | .. | .. | rr |

*List of Plankton Alga-flora* (cont.).

| | River Bure above Wroxham Broad. | Wroxham Broad. | River Bure below Wroxham Broad. | "Upper Salhouse Broad." | Surlingham Broad. | River Yare at Brundall. | Rockland Broad. | Ormesby Broad. |
|---|---|---|---|---|---|---|---|---|
| CHLOROPHYCEÆ (*cont.*). | | | | | | | | |
| PROTOCOCCALES (*cont.*). | | | | | | | | |
| *Cœlastrum sphæricum* Naeg. | .. | c | r | rrr | .. | .. | .. | rrr |
| *Tetrastrum apiculatum* (Lemm.) Schmidle | .. | .. | .. | .. | .. | .. | c | |
| ,, *staurogenieforme* (Schroed.) Lemm. | .. | .. | .. | .. | .. | .. | rrr | |
| ,, *Rocklandensis* sp. nov. | .. | .. | .. | .. | .. | .. | rrr | |
| *Lagerheimia Wratislaviensis* Schroed. | .. | .. | .. | .. | .. | .. | rrr | |
| *Chodatella Droescheri* Lemm. | .. | rrr | | | | | | |
| ,, *longiseta* Lemm. | .. | rrr | | | | | | |
| *Actinastrum Hantzschii* Lagerh. | .. | .. | .. | .. | rr | rr | rrr | |
| *Scenedesmus acuminatus* (Lagerh.) Chod. | .. | r | .. | .. | .. | .. | rrr | r |
| ,, *bijugatus* var. *alternans* (Reinsch) Hansg. | .. | rr | | | | | | |
| ,, *denticulatus* Lagerh. | .. | rrr | | | | | | |
| ,, *Hystrix* Lagerh. | .. | .. | .. | rrr | | | | |
| ,, *obliquus* (Turp.) Kuetz. | .. | .. | .. | rrr | .. | . | r | |
| ,, *opoliensis* P. Richter (?) | .. | .. | .. | .. | .. | .. | .. | rrr |
| ,, ,, var. *carinatus* Lemm. | .. | rr | rrr | rrr | .. | .. | rr | rrr |
| ,, *quadricauda* (Turp.) Bréb. | rr | r | rrr | rr | rrr | rr | rr | |
| ,, *Raciborskii* Woloszynska | .. | rrr | .. | rrr | .. | .. | .. | rrr |
| *Ankistrodesmus falcatus* var. *mirabilis* W. & G. S. West | .. | rrr | | | | | | |
| *Selenastrum Bibraianum* Reinsch | .. | .. | .. | .. | .. | .. | .. | rrr |
| *Tetraedron minimum* (A. Br.) Hansg. | .. | rrr | | | | | | |
| ,, *caudatum* var. *incisum* Lagerh. | .. | rrr | .. | rrr | | | | |
| ,, *limneticum* Borge | .. | .. | .. | .. | .. | .. | .. | rr |
| *Dictyosphærium pulchellum* Wood | rr | rr | .. | r | .. | .. | cc | c |
| *Richteriella botryoides* (Schmidle) Lemm., var. *tetrædrica* Lemm. | .. | .. | .. | r | rrr | rr | rrr | rrr |
| ,, *quadriseta* Lemm. | .. | .. | .. | rrr | | | | |
| *Kirchneriella gracillima* Bohlin | .. | rrr | | | | | | |
| DESMIDIEÆ. | | | | | | | | |
| *Staurastrum tetracerum* Ralfs | .. | rr | .. | .. | .. | .. | .. | rr |
| ,, *paradoxum* Meyen | .. | .. | .. | .. | .. | .. | .. | rrr |
| ,, ,, var. *biradiatum* Griff. | .. | rrr | | | | | | |
| ,, *dejectum* Bréb. | .. | .. | .. | .. | .. | .. | . | r |
| PERIDINIEÆ. | | | | | | | | |
| *Ceratium hirundinella* O. F. M. | .. | .. | .. | .. | .. | .. | .. | rr |
| *Diplopsalis acuta* Entz fil. | .. | .. | .. | .. | .. | .. | .. | rr |
| FLAGELLATA. | | | | | | | | |
| *Dinobryon Sertularia* Ehrenb. | .. | .. | .. | .. | .. | .. | c | |
| ,, *stipitatum* Stein. | .. | c | | | | | | |

## NOTES ON SPECIES.

### Bacillarieæ.

MELOSIRA (ORTHOSIRA) GRANULATA Ehrenb. (von Schoenfeldt, Süsswasserflora, Deutschlands, Osterreichs u. d. Schweitz, x. Bacillarieales, p. 16). The diatom occurred in abundance in Wroxham and Ormesby Broads in association with *Melosira distans*. Under the name of *Orthosira punctata*, n. sp., it is recorded by W. Smith in British Diatomaceæ, ii. p. 62, as from "Ormesby, Norfolk, October and November 1853." It also occurs in some of the larger and deeper Lowland waters (Griffiths, **8**, p. 82), and was found by the writer in 1926 in Upper Bittell Reservoir, a large and deep artificial water near Bromsgrove, Worcs.

MELOSIRA DISTANS Kuetz. The dominant planktont in Wroxham and a co-dominant in Ormesby. Messrs. West record *M. crenulata* Kuetz. (= *M. Binderiana* Kuetz., sec. von Schoenfeldt, *loc. cit.* p. 15) from Lough Neagh. *M. distans* differs from it in having no teeth on the upper edge of the valve face, in being less punctulate, and much broader and shorter.

### Myxophyceæ.

OSCILLATORIA CHALYBEA Mertens (Lemmermann, Kryptogamenflora Mark Brandenburg, iii., Algen I. p. 3). Occurred mainly in River Yare, at Brundall, and also in smaller quantities in Surlingham Broad. Its occurrence is probably due to a combination of sewage effluent and salt-water contamination.

ANABÆNA AFFINIS Lemm. *loc. cit.* pp. 179–183. Occurred only in Ormesby Broad. The variety *intermedia* Griff. is frequent in the plankton of the larger waters of Southern Cheshire, Shropshire, and the Isle of Anglesey (Griffiths, **8**, p. 91). The variety differs from the type only in size.

### Chlorophyceæ.

#### Ulotrichales.

GLOETILIA PROTOGENITA Kuetz. (Heering, in Süsswasserflora, vi. p. 50). Occurred in Wroxham Broad and Upper Salhouse Broad in some numbers. It resembles *Stichococcus scopulinus* Hazen in not having marked constrictions between the cells of the filament, but the size and form of the chloroplast equate it to *G. protogenita*.

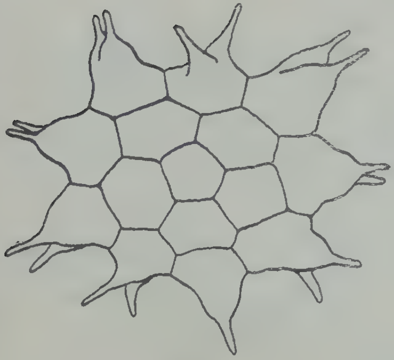
#### Protococcales.

PEDIASTRUM BIRADIATUM Meyen (Brunnthaler, in Süsswasserflora, v. p. 105). Common in Ormesby Broad, and found also in the River Bure, at Wroxham Bridge. It has been found previously in Oss Mere, near Whitchurch, Salop (Griffiths, **8**, p. 84). A typical specimen is shown as fig. 3.

Pediastrum Kawraiskyi Schmidle (Brunnthaler, *loc. cit.* p. 103). This rare species occurred in some numbers in Ormesby Broad. It is peculiar in having the prolongations of the peripheral cells of the cœnobium arranged transversely. It is a rare alga on the Continent, and does not appear to have

Text-figs. 1–4.

(All figures are drawn with the aid of the camera lucida, at a magnification of 650 diameters.)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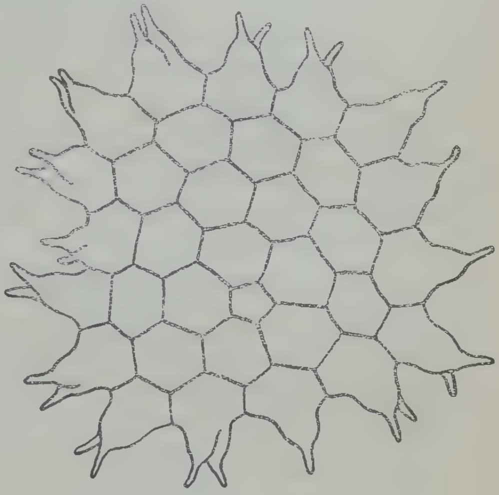
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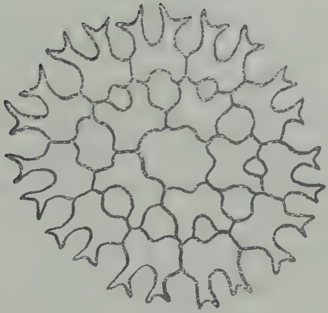
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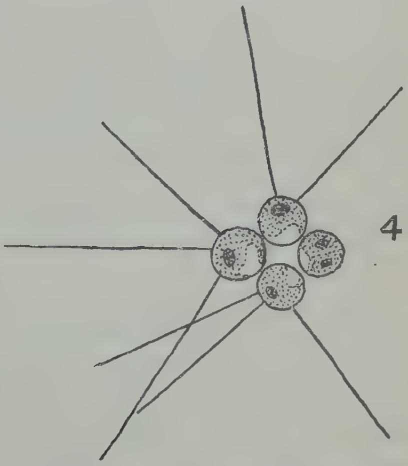
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Fig. 1. *Pediastrum Kawraiskyi* Schmidle, from Ormesby Broad. Cœnobium of fifteen cells.
Fig. 2. " " " " " " Cœnobium of thirty-six cells.
Fig. 3. *Pediastrum biradiatum* Meyen, from Ormesby Broad.
Fig. 4. *Richteriella quadriseta* Lemm., from Upper Salhouse Broad.

been recorded for this country. It is widely distributed, and occurs in the Wisconsin plankton in North America (Smith, G. M., **22**, p. 170, pl. 46. figs. 10–13). Two specimens are shown as figs. 1 and 2.

TETRASTRUM APICULATUM (Lemm.) Schmidle = *Staurogenia apiculata* Lemm. (Brunnthaler, *loc. cit.* p. 177) = *Crucigenia apiculata* (Lemm.) Schmidle (Griffiths, Journ. Linnean Soc., Botany, vol. xliii. 1916, p. 431, pl. 34. fig. 13). The alga occurred in relative abundance in Rockland Broad. It has been recorded by the writer from Wilden Pool, Worcs, under the name of *Crucigenia apiculata* (see above). Wilden Pool is supplied with water from the River Stour.

LAGERHEIMIA WRATISLAVIENSIS Schroeder. Also occurred in Rockland Broad. It is rare, but widely distributed, having been found in Berkshire (Griffiths, **7**, p. 9), Northumberland and Durham (Griffiths, **10**, p. 191), Worcestershire (Grove, Bristol, and Carter, **12**, p. 27), and on the Continent (Brunnthaler, *loc. cit.* p. 136).

CHODATELLA DROESCHERI Lemm. (Brunnthaler, *loc. cit.* p. 139). In Wroxham Broad, but very rare. It differs from *Ch. ciliata* (Lagerh.) Lemm. in having the bristles distributed all over the cell and not only at the poles. It is apparently new to this country, but it is widely distributed and occurs in the Wisconsin plankton, U.S.A. (Smith, **22**, p. 131, *Lagerheimia Droescheri* (Lemm.) Printz.).

CHODATELLA LONGISETA Lemm. (Brunnthaler, *loc. cit.* p. 139). One specimen seen in Wroxham Broad with six polar spines. It is apparently new to Britain ; it also occurs in the Wisconsin plankton.

SCENEDESMUS HYSTRIX Lagerh. (Brunnthaler, *loc. cit.* p. 165). One specimen seen in "Upper Salhouse Broad." The surface of the cell is adorned with very short hair-like processes. The record is apparently new for this country. Again, it is also recorded for Wisconsin.

SCENEDESMUS OPOLIENSIS P. Richter var. *carinatus* Lemm. (Brunnthaler, *loc. cit.* p. 166 ; Smith, G. M., **22**, p. 159, pl. 41. figs. 8–11). This alga is rare, but widely distributed in the area, occurring in Wroxham, Rockland, and Ormesby. I have found it also in Battersea Park Pool, London. In Ormesby one or two specimens were observed where the axes of the two middle cells of the cœnobium were distinctly inclined obliquely, and in parallel, to the axes of the lateral cells, as in the type-form figured by Brunnthaler, p. 164, fig. 228. All other specimens agreed with the variety, and not with the type. Smith, however, figures the variety as the type. These Norfolk specimens agree with his figures.

SCENEDESMUS RACIBORSKII Woloszynska (Griffiths, **6**, p. 433, pl. 34. figs. 7 & 8). This very curious species occurred in small numbers in Wroxham, Upper Salhouse, and Ormesby. The cœnobium was often in a state of division (see figs. 6 & 7). It consists of a group of four slightly lunate cells which adhere by their broad sides instead of by their narrower edges. It differs from *Tetradesmus wisconsinensis* G. M. Smith (Smith, **22**, p. 150, pl. 37. figs. 7–11 ; also Brunnthaler, *loc. cit.* p. 160, footnote) in having a reverse method of aggregation of the cells of the cœnobium. *S. Raciborskii* is not listed by Brunnthaler. I have found it in Wilden Pool, Worcs (see above).

TEXT-FIGS. 5–8.

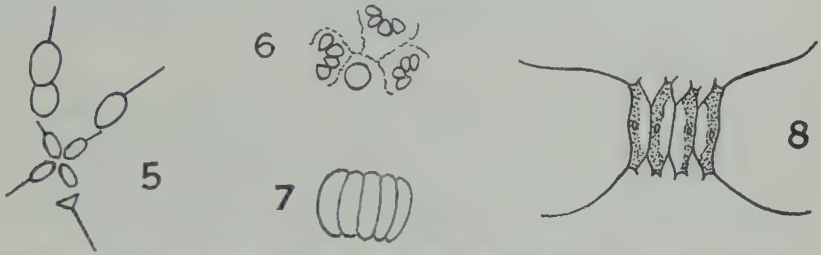

Fig. 5. *Tetrastrum Rocklandensis*, sp. nov., from Rockland Broad. Three cells of the parental cœnobium are figured, and the filial cœnobium derived from the fourth. Close to the young cœnobium there lies the spinous conical apical part of the fourth parental cell.

Fig. 6. *Scenedesmus Raciborskii* Woloszynska, from Ormesby Broad. The figure shows an axial view of a cœnobium in which three of the cells are dividing. The young cells are adhering by their lateral sides to form a packet.

Fig. 7. *Scenedesmus Raciborskii* Woloszynska, from Wroxham Broad. Mature cœnobium, viewed laterally and posteriorly.

Fig. 8. *Scenedesmus opoliensis* P. Richter var. *carinatus* Lemm., from Ormesby Broad.

RICHTERIELLA BOTRYOIDES (Schmidle) Lemm. = *Micractinium pusillum* Fresen (G. M. Smith, *loc. cit.* p. 125). The variety *tetraedrica* Lemm. occurred in the more potamic habitats in this area. The type was not seen, but it occurs in Ryton Willows Pool, Co. Durham, and is also recorded for Worcestershire by Hodgetts (Grove, Bristol, and Carter, **12**, p. 27). Smith says that "the form *tetraedrica* (is) unworthy of recognition," but it seems quite characteristic of this area, though doubtless it shades off into the type elsewhere.

RICHTERIELLA QUADRISETA Lemm. = *R. botryoides* var. *quadriseta* (Lemm.) Schmidle (Brunnthaler, *loc. cit.* p. 119) = *Micractinium quadrisetum* (Lemm.) G. M. Smith (Smith, *loc. cit.* p. 126). One specimen was seen in Upper Salhouse Broad (fig. 4).

### Desmidieæ

STAURASTRUM PARADOXUM Meyen, var. *biradiatum* Griff. (Griffiths, Journ. Linn. Soc., Botany, vol. xlvii. 1925, p. 89, pl. 1. figs. 1–3). This desmid is quite characteristic of the larger and deeper Lowland waters. It appeared in very small numbers in Wroxham Broad, but was not seen in Ormesby.

S. PARADOXUM Meyen and S. DEJECTUM Breb. were both seen in Ormesby Broad, the former in very small numbers and the latter rather more plentifully. Both are desmids of wide distribution.

### Peridinieæ.

CERATIUM HIRUNDINELLA O. F. Mueller. This characteristic planktont of the medium-sized and larger Lowland waters occurred only in Ormesby Broad. It is a rather small variety with only two basal horns, very much like the variety which was found by the writer in Hornsea Mere, Yorks (Griffiths, **9**, p. 246).

DIPLOPSALIS ACUTA Entz. fil. (Schilling, in Süsswasserflora, iii. p. 51) = *Glenodinium acutum* Apstein, in Das Süsswasserplankton, 1896, p. 152 = *Peridinium latum* Paulsen (Nordisches Plankton, viii. Peridiniales, p. 41; also Lemmermann, *loc. cit.* p. 674, figs. 1–7, p. 651). This very interesting Peridinian occurred in fair numbers in Ormesby Broad. It has been recorded for some of the North German lakes, but has not hitherto been found in this country. It is the only freshwater representative of a marine genus. It is shown in figs. 9, 10, 11.

TEXT-FIGS. 9–11.

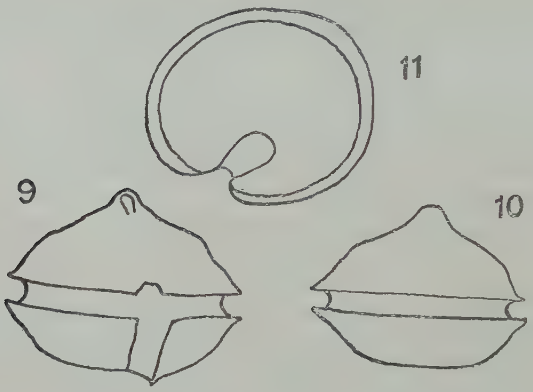

Fig. 9. *Diplopsalis acuta* Entz fil., from Ormesby Broad. Anterior view.
Fig. 10. " " " " " " " Posterior view.
Fig. 11. " " " " " " " Axial posterior view, showing depth of the equatorial furrow and the oblique position of the longitudinal furrow.

TETRASTRUM ROCKLANDENSIS, sp. nov. (fig. 5). One specimen of a species of *Tetrastrum* was observed in the plankton of Rockland Broad. It does not seem to agree with any form previously figured, and it is therefore described here as new. The colony consists of four ellipsoidal cells arranged in a cruciform manner. In the young cœnobium the bases of the cells are adpressed, so that the inner ends of the cells are angulate. Each cell has one apical axial spine, which is as long as or twice as long as the length of the cell. On division, the upper part of the wall of the cell appears to split off as a small conical cap with the spine projecting from the apex (see fig. 5). The diagnosis is as follows :—

*Tetrastrum Rocklandensis*, sp. nov. Cœnobium cruciforme, e quattuor cellulis ellipsoidalibus compositum ; cellula quæque in apice spina axiali armata. Diam. cell. 5–6 $\mu$, long. cell. 7–10 $\mu$ ; long. spinæ 10–14 $\mu$. In plankton Rockland Broad, Norfolk, England.

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# Resin Canals in Seedling Conifers.

By CHARLES S. HANES, Research Student of Downing College, Cambridge. Exhibition of 1851 Research Scholar. [Communicated by Professor A. C. SEWARD, F.R.S., F.L.S.]

(PLATE 37 and 20 Text-figures.)

[Read 12th May, 1927.]

THE present account is concerned mainly with the primary resin canals of conifers, as distinct from canals occurring in tissues of cambial origin. Most of the observations have been made on seedling material, but where possible these have been supplemented by comparison with adult organs. In recent years considerable attention has been given to the resin-secreting structures in this group of plants: most investigators, however, have confined their studies to the resin canals in the secondary wood. The literature lacks comparative accounts of the primary resin canals, as most of the recorded data are incidental to the description of other features. It is hoped that the present account may help to fill in this gap, and give a more complete picture of the resin-secreting structures of the Conifers.

Some authors tend to emphasize the importance of the structure and distribution of resin canals as a clue to phylogeny. The writer hesitates to assign any such significance to the data on primary resin canals now presented. It is felt that much more must be known about the factors governing the secretion of resin before the character of resin canals can be interpreted as phylogenetic evidence.

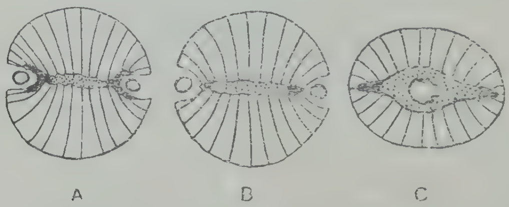
Many species of Coniferæ have been examined, and I am deeply indebted to the many persons who have supplied material, especially to Dr. A. W Hill, the Director, Royal Botanic Gardens, Kew, and to Mr. H. Gilbert-Carter, the Director, Cambridge Botanic Garden. I am also very grateful to Mr. T. G. Hill, of University College, London, who has been very helpful, and has kindly permitted me to use his extensive collection of serial sections of conifer seedlings. These preparations have greatly facilitated the work.

## DESCRIPTION OF THE PRIMARY RESIN CANALS.

### Tribe ABIETINEAÆ.

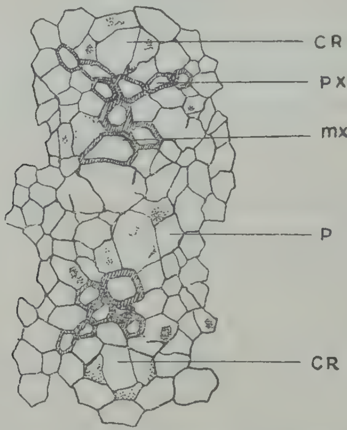
It has been known for many years that the Abietineæ have primary resin canals in their roots. The canals are of two types, which will be referred to as the root-pole canals and the central canals. Root-pole canals are closely associated with primary xylem poles, and occur in the roots of the genera *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*. Central canals, on the other hand, occur in the middle of the metaxylem, in the roots of *Abies*, *Cedrus*, *Pseudolarix*, and *Tsuga*. Van Tieghem (1872, p. 194) recognized these features, which are later referred to by Jeffrey (1905) when he proposed the division of the Abietineæ into the two subfamilies Pineæ and Abieteæ. Text-fig. 1 shows the position of the two types of primary root canal.

Text-fig. 1.



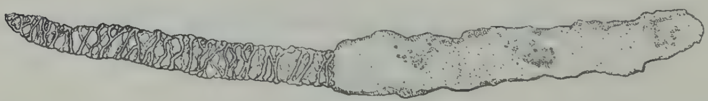
Roots of Abietineæ, showing root-pole canals in A (*Pinus*) and B (*Picea, Larix,* and *Pseudotsuga*); central root canal in C.

Text-fig. 2.



Transverse section of a small root of *Pinus sylvestris*. (× 280.) CR, root-pole resin canal *px*, protoxylem; *mx*, metaxylem; P, undifferentiated tissue.

Text-fig. 3.



Composite structure from the root-pole region of a *Pinus Strobus* root. (× 280.)

Root-pole canals lie close to the protoxylem plates of the root, and in the genus *Pinus*, where the protoxylem differentiates as a Y-shaped strand, the resin canal lies in the angle of the Y (text-fig. 1, A, and text-fig. 2). In the upper resin canal in text-fig. 2 a xylem element abuts directly upon the lumen of the canal, which is an unusual feature. Lower down in the same series of sections this xylem element was continuous longitudinally with a parenchyma cell. It is probable that this structure is of the type shown in text-fig. 3. Several of these composite structures were found in strands of tissue from the region of the primary canals of *Pinus Strobus* roots. The tissue was softened in an aqueous solution containing 5 per cent. nitric acid and 5 per cent. chromic acid, and then teased out on a slide.

Root-pole canals of older roots are shown in microphotographs 1 and 2 (Pl. **37**).

There is considerable variation in the upward extent of root-pole canals in different species: in some species of *Pinus* they extend up into the cotyledons; in other species of *Pinus* and in the genera *Picea*, *Larix*, and *Pseudotsuga* they end at lower levels in the hypocotyl and root. This is shown in the following table :—

| | |
|---|---|
| *Pinus australis.* | The root-pole canals extend more than halfway up the cotyledons. |
| *P. insignis.* | |
| *P. Murrayana.* | |
| *P. sylvestris.* | The root-pole canals end in the bases of the cotyledons. |
| *P. excelsa.* | The root-pole canals end in the upper region of the hypocotyl. |
| *P. Strobus.* | |
| *P. halepensis.* | |
| *P. maritima.* | |
| *P. Coulteri.* | |
| *P. pinea.* | |
| *P. Gerardiana.* | |
| *Larix.* | The root-pole canals end in the lower region of the hypocotyl. |
| *Picea.* | |
| *Pseudotsuga.* | |

In the genera *Abies, Cedrus, Tsuga,* and *Pseudolarix* the roots have primary resin canals of the central canal type. These are not so regular in distribution, and will be mentioned in the descriptions of the particular species.

## Genus Pinus.

### Pinus australis.

Serial sections of two seedlings were examined. Each of the cotyledons has a root-pole canal (text-fig. 4). In the figure, canals from two adjacent cotyledons are shown joining together at the cotyledonary node to form one root-pole canal. The vascular strands of cotyledons undergo various transitions in their course into the root. Hill and de Fraine (1908) suggest the following terminology : a whole-cotyledon is one whose vascular strand descends to form one pole of the root structure (text-fig. 5); a half-cotyledon

TEXT-FIG. 4.

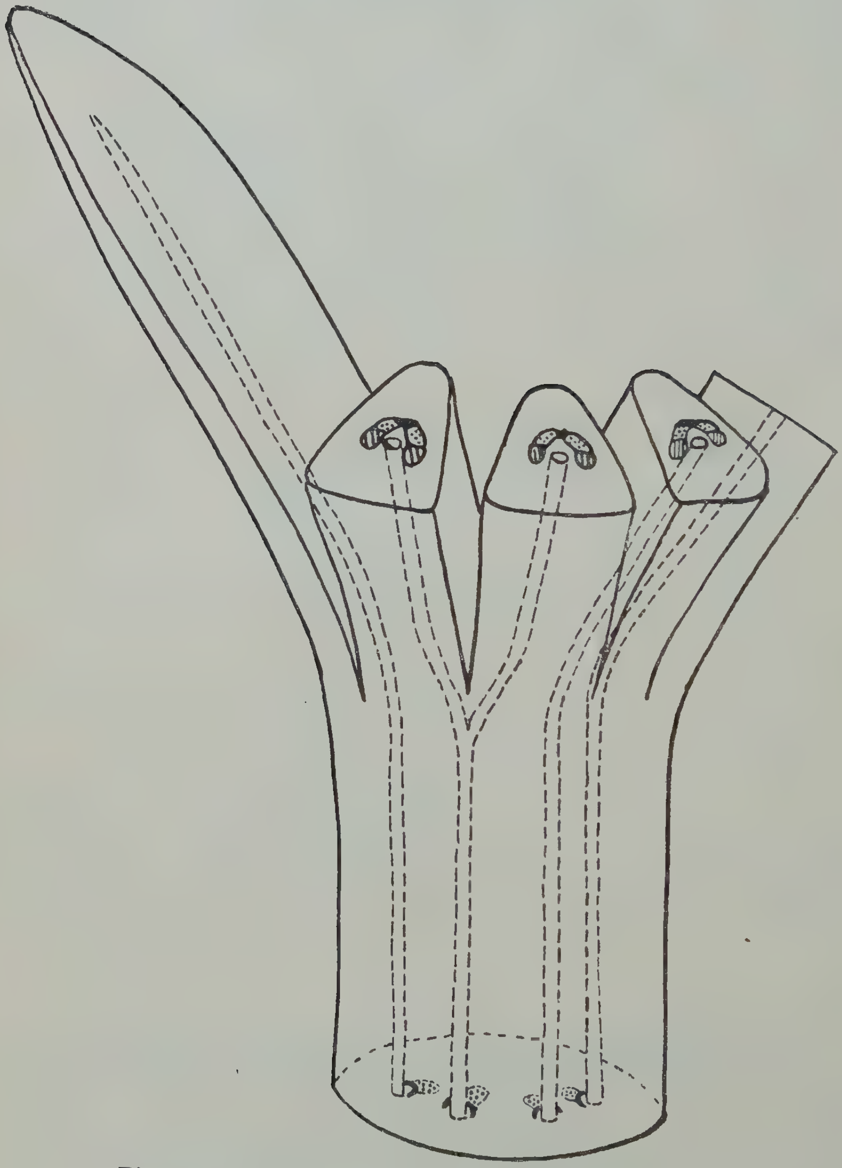


Diagram showing the cotyledonary node in *Pinus australis*. The root-pole resin canals are shown in dotted lines.

is one whose vascular strand corresponds to only one-half of a root-pole, in which case the root-pole bundle is bifurcated, a branch going to each of two adjacent half-cotyledons; the vascular strands of some cotyledons take no part in the formation of the root structure, and these are called subsidiary cotyledons. The half-cotyledons of *Pinus australis* possess branches of root-pole canals, as in text-fig. 4.

TEXT-FIG. 5.

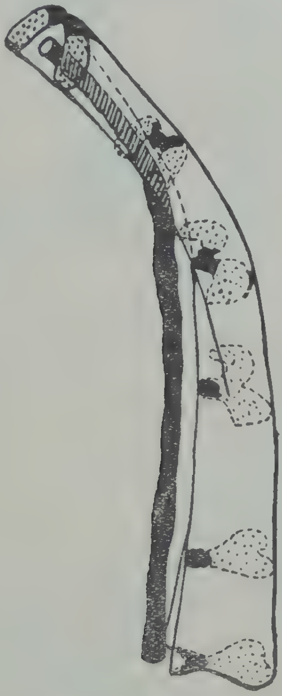
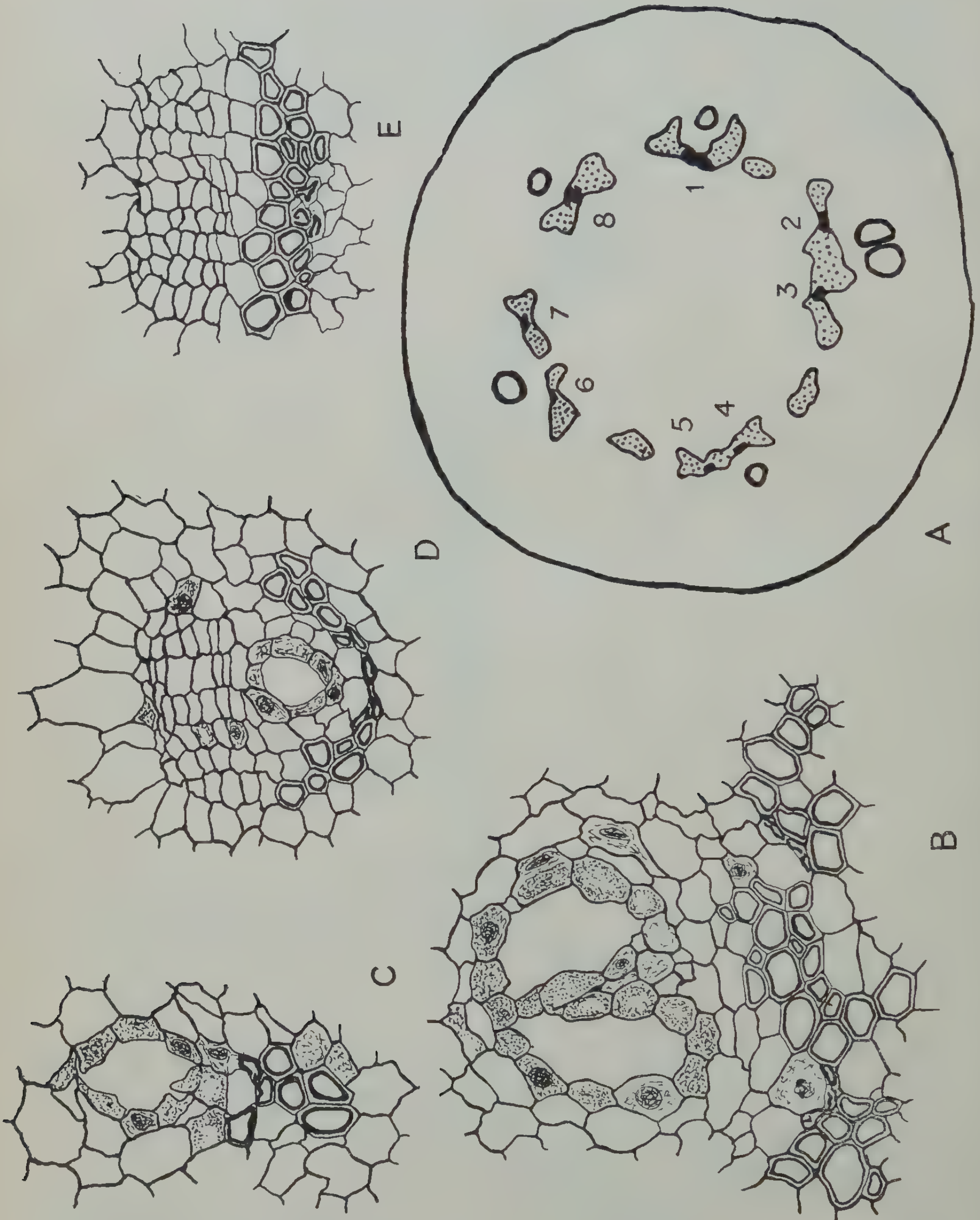


Diagram of cotyledonary bundle in the transition region between the exarch structure in the root and the endarch in the cotyledon. The root-pole canal is shown in black; protoxylem black; metaxylem dotted.

### PINUS INSIGNIS.

Text-fig. 4 will also serve for this species. Two seedlings were studied. One had five whole-cotyledons, each of which had a root-pole canal. In the other seedling there were eight cotyledons (text-fig. 6, A). The numbers 1 to 8 in this diagram represent the vascular strands of the cotyledons. Nos. 1 and 8 are whole-cotyledons, and all the others are half-cotyledons. All have root-pole canals except No. 5. Other drawings in text-fig. 6 show vascular strands with associated root-pole canals at different levels in the seedling.

Text-fig. 6.

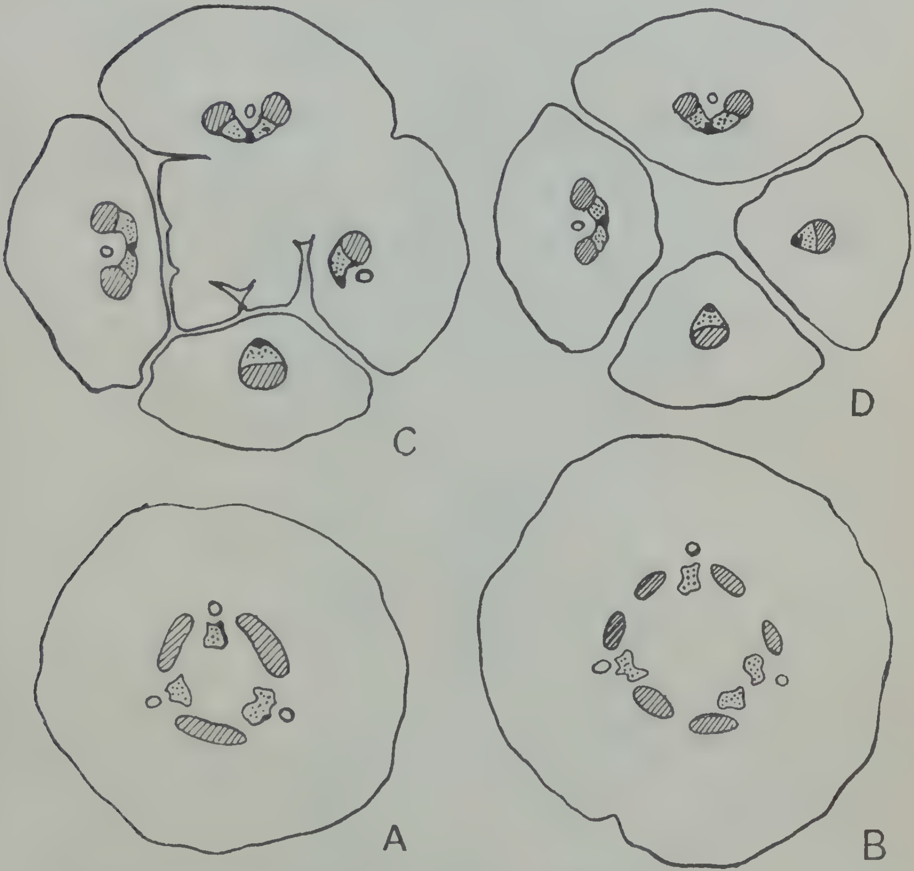


*Pinus insignis.* A. Diagram of transverse section of cotyledonary node. Nos. 1–8 are cotyledonary traces. 1 and 8 are whole-cotyledons; all the others are half-cotyledons. B, C, D, and E show vascular strands (× 250). B, level of cotyledonary node; C, in lower part of hypocotyl; D & E, halfway up cotyledons 4 and 5. (No. 5 has no root-pole canal.)

PINUS MURRAYANA (var. SARGENTI).

Five seedlings were used whose cotyledons varied from three to five in number. In four seedlings all the cotyledons were whole-cotyledons, and in these root-pole canals extended up about one-quarter of their length. The other seedling had two whole-cotyledons and two half-cotyledons (text-fig. 7).

TEXT-FIG. 7.



*Pinus Murrayana.* Sections at various levels (× 30). A, lower hypocotyl; B, upper hypocotyl; C, cotyledonary node; D, slightly above C.

In each of the whole-cotyledons, which are considerably larger than the others, the canal extends to the tip. The smaller of the two half-cotyledons has no root-pole canal, while the larger one has only a short canal.

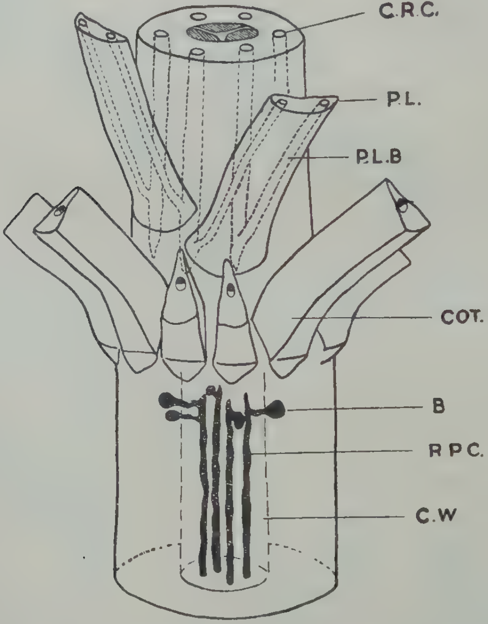
PINUS SYLVESTRIS.

Hill and de Fraine (1909) and Chauveaud (1911) have described the vascular anatomy of this species, and have recorded the presence of short resin canals in the bases of the cotyledons. These short root-pole canals are often absent from half-cotyledons.

PINUS EXCELSA, P. STROBUS, P. HALEPENSIS, P. MARITIMA, and P. COULTERI.

These species have no canals in their cotyledons. The root-pole canals end in the upper part of the hypocotyl, as is shown in text-fig. 8. This diagram is based on *Pinus excelsa*. At their upper ends the root-pole canals have numerous horizontal canals associated with them leading out to bulb-like expansions beyond the cambium. These structures were also observed in *P. Strobus* and *P. maritima*, but the available seedlings of *P. halepensis* and *P. Coulteri* were too young to show them. These horizontal canals are embedded in medullary rays, and they connect openly with the root-pole canals. The bulbs are formed from the cambium, and as they develop are pushed out into the primary cortex. Several of these structures are shown in photomicrographs 3 and 4 (Pl. **37**). They seem similar to the horizontal canals originating from the vertical canals in the secondary wood of stems and roots, as described by Thomson and Sifton (1925). Further reference to these horizontal canals ending in bulbs is made later in the concluding discussion.

TEXT-FIG. 8.



*Pinus excelsa.* Diagram of cotyledonary node with epicotyl. The root-pole canals (R.P.C.) are connected with horizontal canals at their upper end. The horizontal canals end in bulbs (B) outside the cambium (C.W.). COT., cotyledon. C.R.C., P.L., P.L.B. are explained in the text.

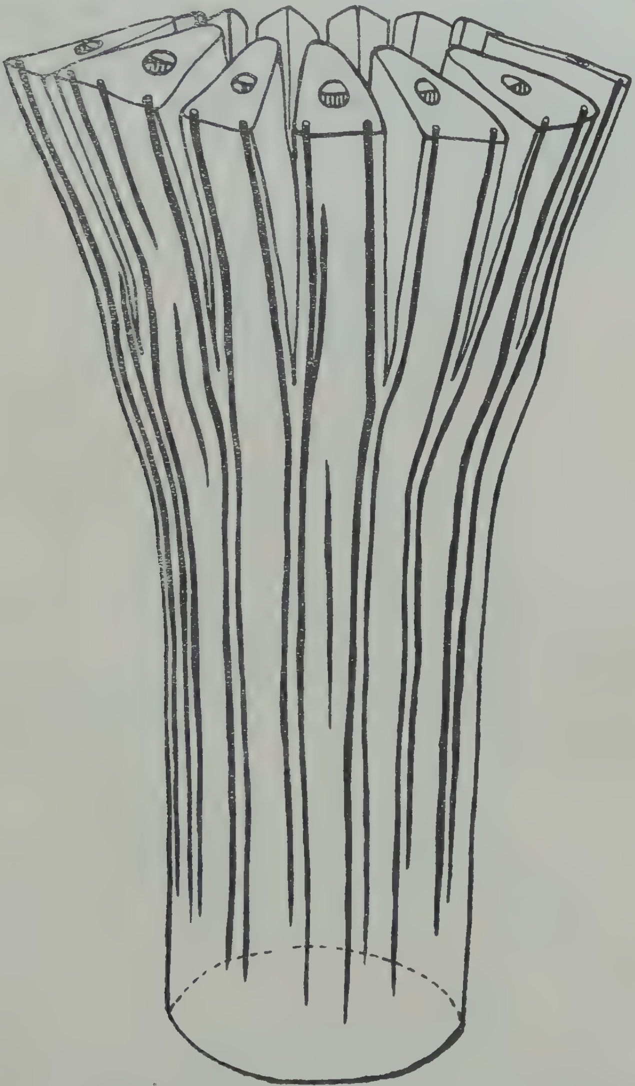
PINUS PINEA, P. CANARIENSIS, P. GERARDIANA, and P. EDULIS.

The cotyledons of these species have no root-pole canals, but there are other resin canals lying in a more superficial position which will be referred to as corner canals.

PINUS PINEA.

About sixty seedlings of this species were examined. Serial sections were made of six of these; the rest were observed under the binocular microscope, which reveals the course of the corner canals. Each cotyledon has a pair of these canals, which lie close beneath the surface, one in each of the outer corners of the cotyledon (text-fig. 9). They extend from the tips of the cotyledon downwards an inch or more into the hypocotyl, where they tend to be arranged in pairs.

TEXT-FIG. 9.



*Pinus pinea.* Diagram of the cotyledonary node showing the corner canals.

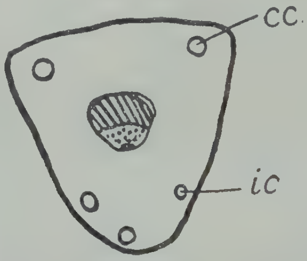
Many minor variations from the regular pattern occur, as is shown in text-fig. 9. In one specimen the two corner canals from adjacent cotyledons joined together and continued down the hypocotyl as a single canal. One small cotyledon had only one corner canal. Occasionally small additional canals are present, either as branches of corner canals or lying separately.

The canals develop at a very early stage, as was found from sections of a seedling still enclosed within the endosperm.

### PINUS CANARIENSIS.

This species also has corner canals which continue down the hypocotyl. In addition, however, there are other superficial canals along the inner surfaces of the cotyledons. These are very short and do not continue into the hypocotyl (text-fig. 10).

TEXT-FIG. 10.



*Pinus canariensis.* Transverse section of a cotyledon. *cc,* corner canals; *ic,* canals along inner surfaces.

### PINUS GERARDIANA.

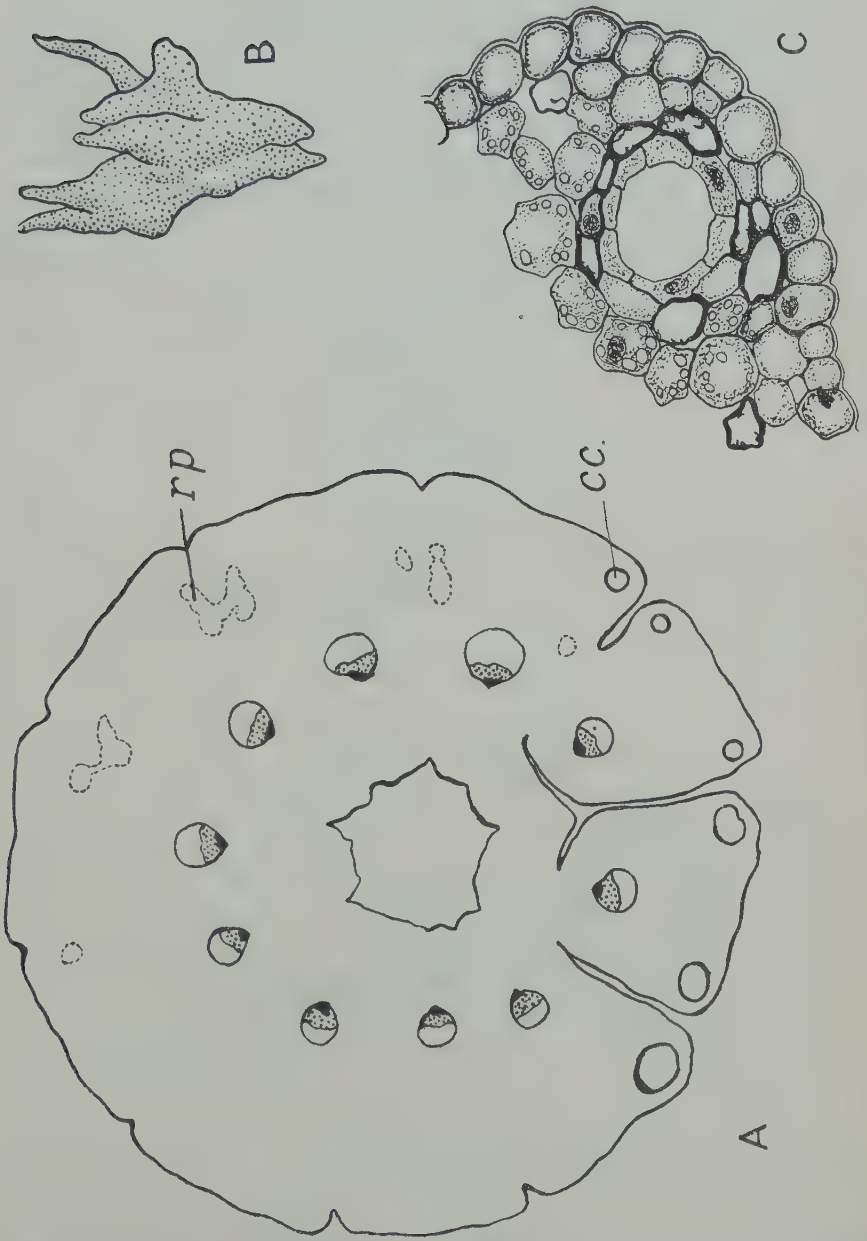
Twelve seedlings were sectioned. Corner canals are present, as in *P. pinea*, but they end at the bases of the cotyledons, the hypocotyl having no cortical resin canals. Below the lines of junction of adjacent cotyledons there is a series of small cysts, or resin-pockets, shown in transverse section in text-fig. 11, A. A drawing of one of these, reconstructed from serial sections, is seen in text-fig. 11, B.

## *The Stem and Leaves of* Pinus.

The epicotyl of a pine seedling is thickly covered with juvenile leaves arranged in a close spiral. Each leaf has two resin canals which lie in the mesophyll, one at each side of the vascular bundle. The position of these canals varies slightly in different species. The following description is based on *Pinus excelsa.*

The epicotyl, in transverse section, shows a ring of six conspicuous longitudinal resin canals in its cortex (text-fig. 8, C.R.C.). The leaf-traces pass out between them. At the base of each juvenile leaf (P.L.) a branch canal (P.L.B.) arises from each of the two adjacent longitudinal canals of the epicotyl, and these two branches continue out into the leaf, forming the lateral canals in the mesophyll. This is shown in text-fig. 8 and also in

Text-fig. 11.

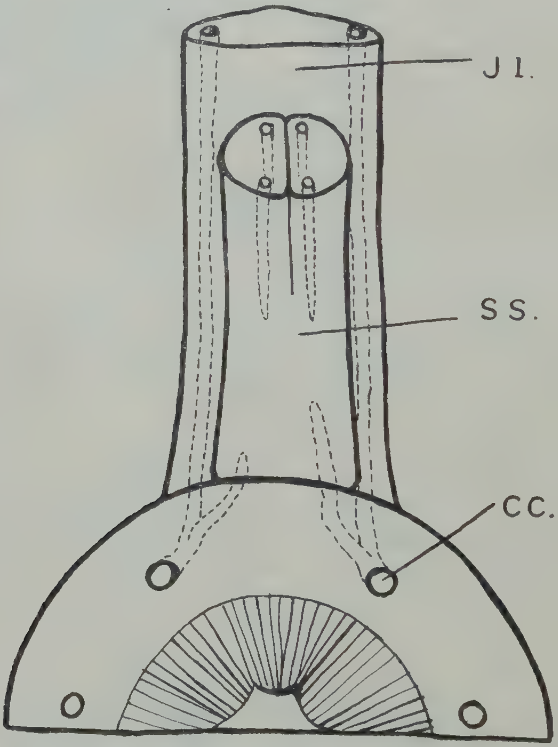


*Pinus Gerardiana.* A is a slightly oblique section through the cotyledonary node. *cc*, corner canals; *rp*, resin cysts. B shows a reconstruction of one of the cysts (*rp*). C, a corner canal (× 250). The dark cells without content are so-called tannin sacs.

microphotograph 5 (Pl. **37**). In this section three longitudinal canals of the epicotyl are shown, with leaf-traces from two juvenile leaves between them: four smaller canals, the lateral canals of the two leaves, are cut in various stages of separation from the cortical canals.

The cortical canals of the epicotyl end blindly above the cotyledonary node. They do not connect with any lower resin canals. Moreover, the cortical canals of each year's growth in length form separate systems which do not connect with the canals in the cortex above or below. The number of canals which form in the cortex increases as the growing point of the stem becomes older.

TEXT-FIG. 12.



*Pinus Pinaster*, young stem axis. Diagram of spur shoot in axil of a juvenile leaf. *ss.*, spur shoot ; *jl.*, juvenile leaf ; *cc.*, cortical canal of young stem.

The resin canals in the adult leaves of *Pinus* have been dealt with by many investigators. The number and position of canals varies considerably in adult leaves of the same species. There is, however, a tendency to have two lateral canals, which are more constant than the others, and in some species more prominent. The resin canals of pine needles have not been seen to connect with the cortical canals of the stem, even when spur shoots occur on very young stems in the axils of juvenile leaves. Such an instance is shown in text-fig. 12, which is based on data from serial sections of a young stem of *Pinus Pinaster*. Short branches from the cortical canals run into the base of the spur shoot, but these do not connect with the adult leaf canals. The lateral canals of the juvenile leaf are connected with the stem canals, as was mentioned above. Spur shoots in *P. Strobus* and *P. Laricio* were similar.

### Genus PICEA.

PICEA EXCELSA, P. AJANENSIS, P. NIGRA, P. MORINDA, and P. ALBA.

These are all similar in the distribution of resin canals. The cotyledons are small and have no resin canals. The root-pole canals do not extend above the root. In three-year-old plants of *Picea excelsa* and *P. Morinda* the upper endings of the root-pole canals were about two inches below the cotyledonary traces.

### Genus LARIX.

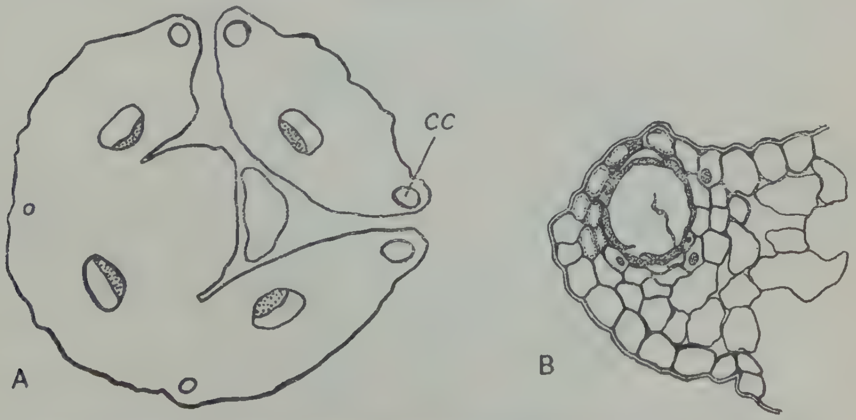
LARIX OCCIDENTALIS and L. LARICINA.

There are no resin canals in the cotyledons. The root-pole canals end in the lower part of the hypocotyl.

LARIX LEPTOLEPIS.

The two specimens examined had each four cotyledons, and in all of these there are short corner canals. The canals are very irregular and do not extend into the hypocotyl.

TEXT-FIG. 13.



*Abies balsamea.* A, section through cotyledonary node, showing corner canals, *cc.* B, a corner canal (× 250).

### Genus ABIES.

ABIES BALSAMEA, A. VEITCHEI, A. NEPHROLEPIS, and A. MAGNIFICA.

In these species corner canals are present in the cotyledons. These canals do not extend below the cotyledonary node; they lie very close to the epidermis (text-fig. 13).

ABIES SIBIRICA.

In the single specimen available there are corner canals as in the preceding species. There is also a series of cysts situated below the lines of junction of adjacent pairs of cotyledons as in *Pinus Gerardiana.* These were not seen in any other species.

ABIES PECTINATA.

There are no resin canals in the cotyledons, which are small.

### Genus CEDRUS.

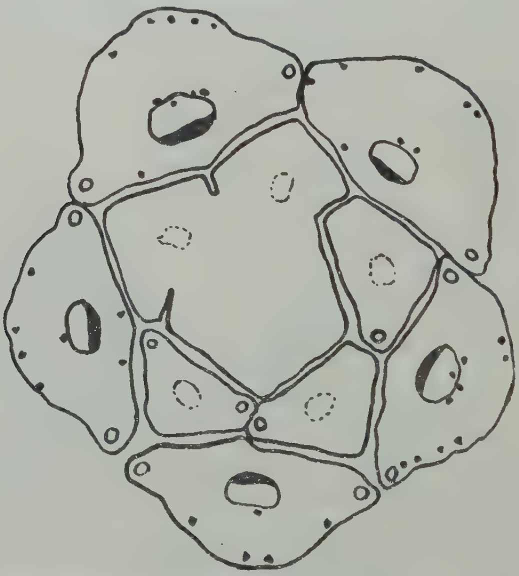
CEDRUS DEODARA.

Two seedlings, each of which had eleven cotyledons, were examined. The extent of the canals in these is varied; some of the canals do not extend higher than halfway up the cotyledon, while others are confined to the upper part of the cotyledon.

CEDRUS ATLANTICA.

No resin canals were seen in the cotyledons. Otherwise the seedlings are very similar to *Cedrus Deodara.*

TEXT-FIG. 14.



*Pseudolarix Kaempferi.* Section through cotyledons and leaves of the plumule. The small black dots represent tannin sacks.

### Genus PSEUDOLARIX.

PSEUDOLARIX KAEMPFERI.

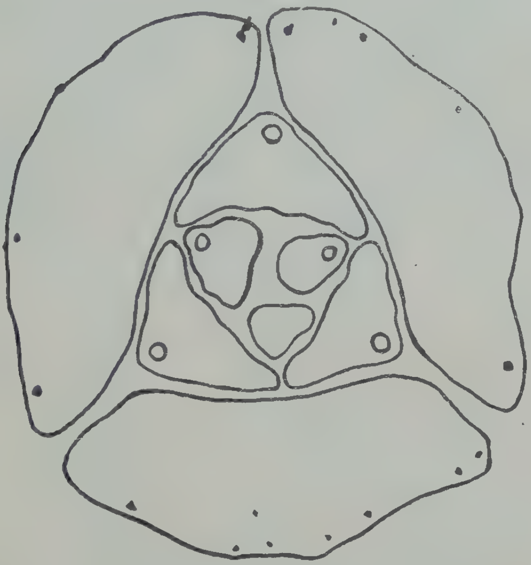
Two seedlings had each five cotyledons. Corner canals are present extending to the base of the cotyledons (text-fig. 14).

### Genus Tsuga.

Tsuga diversiflora and T. canadensis.

There are no canals in the cotyledons. The leaves of the plumule have a single canal which runs centrally beneath the midrib (text-figs. 15 & 16). These midrib canals extend down into the bases of the leaves, where they end blindly. This is also the condition in adult leaves. Longitudinal cortical canals are not present in the stem. Thus *Tsuga* differs from the other Abietineæ.

Text-fig. 15.



*Tsuga canadensis.* Section through cotyledons and plumulary leaves. (Black dots are tannin sacks.)

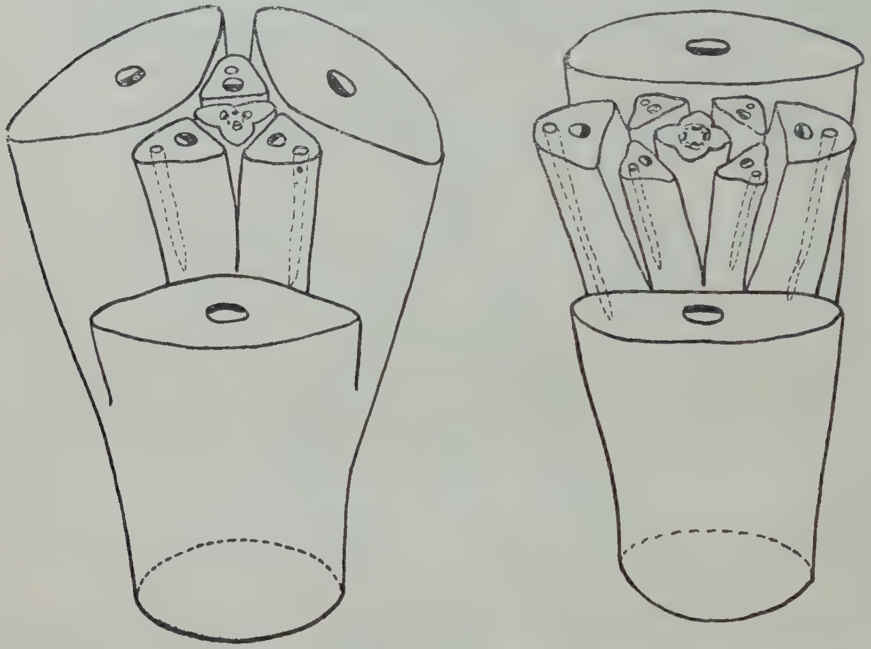
### Tribe **CUPRESSINEÆ.**

*Juniperus oxycedus.*
,, *bermudiana.*
*Widdringtonia Whytei.*
,, *Mahoni.*
*Actinostrobus pyramidalis.*
*Thuja occidentalis.*
*Libocedrus decurrens.*
*Cupressus Lawsoniana.*

*Cupressus torulosa.*
,, *obtusa.*
*Callitris robusta.*
,, *verrucosa.*
,, *Muelleri.*
,, *calcarata.*
,, *rhomboidea.*
,, *australis.*

The distribution of resin canals in all these species is similar (text-fig. 16). It is the same as in *Tsuga*. (The adult leaves of many Cupressinean species are very different in form from the juvenile leaves, and in these a corresponding difference is resin canal distribution occurs.)

TEXT-FIG. 16.



Seedlings of the Cupressinean type. Diagrams of the cotyledonary nodes of seedlings with two and three cotyledons.

## Tribe TAXODINEÆ.

### CRYPTOMERIA JAPONICA.

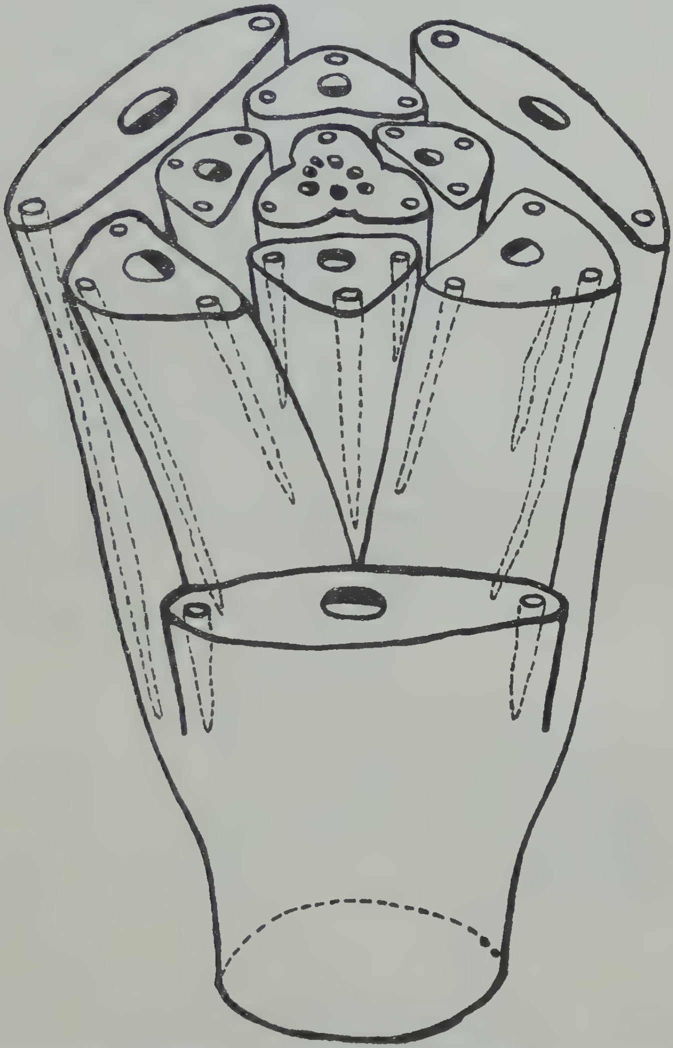
Two seedlings were examined, each of which had three cotyledons. These contain a pair of corner canals ending in their bases. The hypocotyl has no resin canals. The juvenile leaves have not only corner canals which are short, but also midrib canals (text-fig. 17). The adult leaves are reduced and spine-like, and in these only the midrib canal is present, extending down into the leaf-base.

Leaves of the juvenile variety (*C. japonica* var. *elegans*) have both the midrib and corner canals as in the juvenile leaves of the seedling.

### SEQUOIA GIGANTEA.

The cotyledons show a new feature. They have midrib canals which extend down to the lower part of the hypocotyl, where they end blindly. These canals are embedded in the cortical tissues, and are not comparable with the root-pole canals in the cotyledons of some species of *Pinus*. The juvenile leaves of the available seedlings had not yet developed resin canals, as they were very young. Adult leaves are similar to the cotyledons, having canals in the midrib position.

TEXT-FIG. 17.



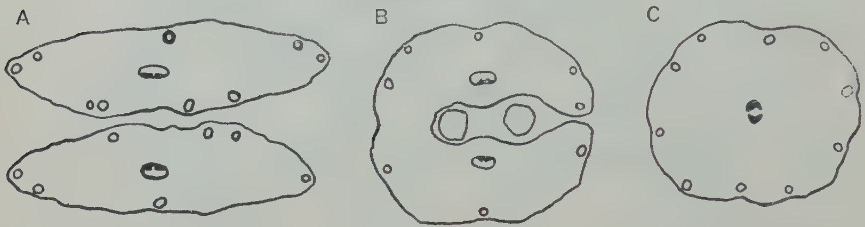
*Cryptomeria japonica.* Diagram of cotyledonary node showing cotyledons with corner canals; plumulary leaves with corner and midrib canals.

Four seedlings were studied. There are two cotyledons which are broad and flat. These have no resin canals. The juvenile leaves have a midrib canal, ending in the bases. Adult leaves have midrib canals and corner canals. The latter are very short, and do not continue down to the base of the leaves.

Sciadopitys verticillata.

The seedlings have two broad cotyledons. Numerous superficial canals are present along both surfaces (text-fig. 18). The canals of the inner surfaces are very short; the outer ones are longer, and some of them extend down the hypocotyl. Thus the hypocotyl has eight or ten superficial canals running to its base.

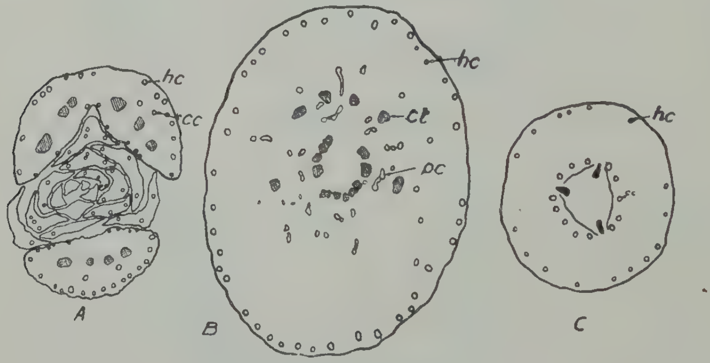
Text-fig. 18.



*Sciadopitys verticillata.* Sections at different levels of a seedling. A, lower part of cotyledons; B, at the cotyledonary node; C, halfway down the hypocotyl.

The juvenile leaves usually have three canals lying close to the epidermis in the midrib and corner positions. These are variable; sometimes there are as many as five such canals; there are often smaller ones along the inner surfaces also, as in the cotyledons.

Text-fig. 19.



*Araucaria imbricata.* Sections through seedlings. A, cotyledons and plumulary leaves B, upper level of hypocotyl; C, the root.

## Tribe TAXINEÆ.

Taxus baccata and T. cuspidata.

Resin canals not present in these species.

Cephalotaxus pedunculata, C. Fortunei, and C. drupacea.

The distribution of canals in the seedlings is the same as in the Cupressineæ (text-fig. 16).

### Tribe ARAUCARINEÆ.

ARAUCARIA IMBRICATA.

There are numerous superficial canals under the outer surfaces of the fleshy cotyledons. These extend down to the lower part of the carrot-like hypocotyl. A few smaller and very short canals occur along the inner surfaces of the cotyledons.

Numerous irregular canals are deeply embedded in the cortex; a few of them extend into the basal part of the cotyledons down the hypocotyl, and continue, greatly reduced in number, into the root (text-fig. 19).

## DISCUSSION OF THE ANATOMICAL DATA.

Seedlings of the same species of Conifer show the same general distribution of primary resin canals with only minor individual variations. Different species of the same genus are often very different in canal distribution, especially in the case of cotyledonary canals; juvenile leaves, with few exceptions, are constant within a genus.

Among the Abietineæ there is a wide variation in the distribution of resin canals. In the thirty-one species examined the cotyledons of seventeen have no resin canals; eleven have corner canals; three (*Pinus*) have upward extensions of the root-pole canals. In all genera except *Tsuga* the juvenile leaves have two lateral resin canals. In species with adult leaves of the same general shape as the juvenile leaves the former also have two lateral canals. There is deviation from this arrangement in adult leaves which are very different in shape from the juvenile form.

The Cupressineæ present a uniform picture. In all the species examined there are no canals in the cotyledons, and the juvenile leaves have a single midrib canal. This distribution also occurs in the Abietineæ (*Tsuga*), Taxineæ (*Cephalotaxus*), and Podocarpineæ (*Podocarpus*).

The Taxodineæ are represented by only five species from three genera. No two species have a similar distribution of resin canals. The presence of both midrib and lateral canals in *Cryptomeria japonica* and *Sequoia gigantea* is worthy of note.

It is obvious that the number and distribution of these primary resin canals cannot be used as a criterion of relationship even between genera of Coniferæ, since these characters are often very different in species of the same genus. This is made more evident by instances in which a particular type of resin-secreting structure occurs in only a very small number of species which may be obviously not closely related: there are cysts lying below the lines of junction of adjacent cotyledons in *Pinus Gerardiana* and *Abies sibirica*, but in no other species of these genera; superficial cortical canals are present in the hypocotyl of *Pinus pinea*, *P. canariensis*, *Sciadopitys verticillata*, and *Araucaria imbricata*.

## The Formation of Resin Canals.

The resin canals which have been described, except those in *Araucaria*, are formed as intercellular spaces, and not by the breakdown of cells, at least in the young stages studied. The canals develop in the cotyledons of seedlings early in germination. In several seedlings these developing canals showed that actual cell-division was taking no part in the differentiation of the lumen. This is best explained by reference to text-fig. 20. The cells in these sections form a cord of tissue in which a resin canal is developing. The drawings are at different levels in a series of sections of the cotyledon of *Cedrus deodara*, and they are numbered in their order in the series. Cells of similar cross-section recur at successive levels. These are not sections of the same cell, but of cells of the same longitudinal row. It is evident that no cell-division has taken place in the change from a solid cord of tissue into the resin canal with a considerable lumen, since there are no interruptions in the arrangement of the cells in longitudinal seriations. Consequently the prevalent conception that the formation of resin canals is due to cells dividing and pulling apart is inadequate. In the later development of resin canals there is often considerable cell-division, sometimes giving rise to a many-layered sheath about the canal. Thomson and Sifton (1925) describe structures of this kind. Obviously, however, it becomes necessary to look for some new factor to account for the appearance of a lumen in the young developing resin canal. It is suggested that the actual pressure of the fluid resin may play an important part in this differentiation.

The corner canals in the cotyledons of *Pinus pinea*, even in very early stages of the formation of the lumen, are filled with the secretion. This has also been established by Hannig (1922) in canals in leaves of *Abies grandis*. The method was to fix the material in Hannig's fixative (1 per cent. chromic acid solution, saturated with copper acetate) for two days, wash in water, section in water, and mount in glycerine. In this treatment the protoplasm is fixed, and at the same time a green or blue-green colour is given to resin*. Even the very young canals are filled with resin. It is evident, therefore, that the formation of the lumen of a resin canal is associated from early stages with the secretion of resin, and it is suggested that the pressure of secretion is the cause of the pushing apart of the cells to form the lumen.

The existence of a pressure is easily demonstrated in such canals as the

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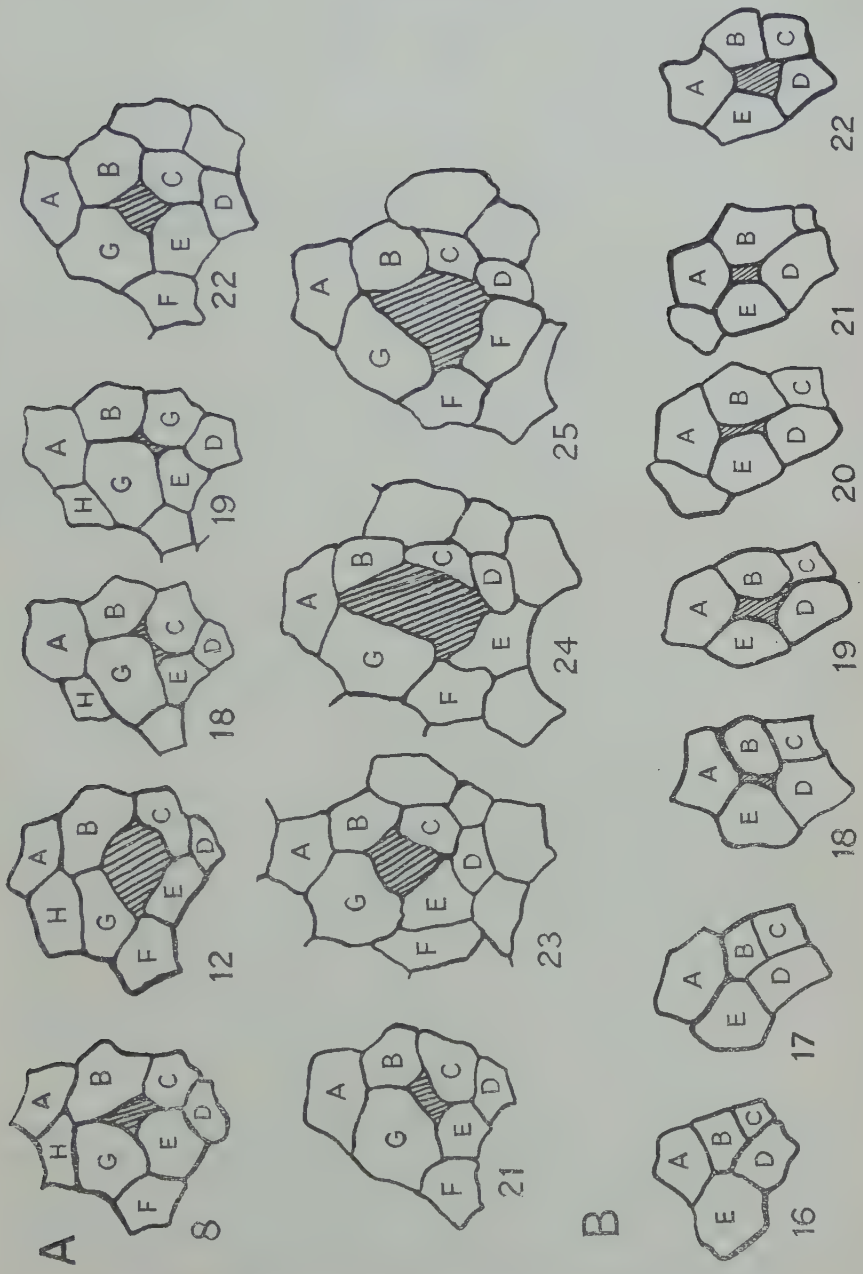
* This colour is presumably due to the formation of copper salts of organic acids of more or less complex composition. Copper salts of the fatty acids of ordinary washing-soap were prepared by adding copper-sulphate solution to a soap suspension. There is a heavy green precipitate, whose solubilities are similar to those of the green colouring matter formed in resin by the action of copper-acetate solution.

TEXT-FIG. 20.



*Cedrus Deodara.* Drawings from series of sections showing developing corner canals. The numbers indicate the order in the series. Description in the text.

corner canals of a cotyledon of *Pinus pinea.* This is done by dissecting away under a binocular microscope the soft tissue surrounding a canal; the canal is then pricked with a fine needle. A drop of resin immediately forms at the puncture. This occurs in various stages of development. A more striking illustration is found in the blister-like swellings of the cortex of *Abies balsamea.* These blisters of resin are formed as swellings of the cortical resin canals. They become noticeable on the surface only on parts of the stem which are at least five or six years old; the size increases with age, so that blisters an inch across are common on old trunks. These structures are very turgid at all stages; if they are punctured, there is an immediate flow of resin from the opening. It seems probable that the gradual accumulation of resin secreted into the lumen distends the walls of the canals at points of weakness.

The shape of a resin-containing structure is related to the grain of the tissue in which it lies. When the tissue is composed of elements elongated in one direction or arranged in longitudinal rows, then the resin lies in a canal running in the longitudinal direction. This is true not only of the primary canals, but also of the canals in the secondary wood and medullary rays.

Mention has already been made of the peculiar bulb-like structures in the bast which terminate horizontal canals from medullary rays. These horizontal canals may take origin either from the root-pole canals, as has been described in *Pinus,* or from vertical canals of the secondary wood. It is possible that these bulbs may be formed by the action of the resin secreted by the canals in the xylem. These cannot increase in volume owing to the firmness of the matrix about them, and consequently excess resin is pressed outwards through horizontal canals. Several stages in the development of these structures are shown in photomicrographs 3 and 4 (Pl. **37**). In these the lumen of the canal is open across the cambial zone, and the resin mass is continuous from the root-pole canal to the bulb in the bast. (Thomson and Sifton have described these structures in *Picea canadensis*; they find that the lumen of the horizontal canal in older stems is often closed at the cambium. This is possibly because the vertical canals, from which the horizontal canals have come, may be old and the secretion of resin into them may have diminished or ceased.)

Up to the present it has not been possible to test experimentally the hypothesis which has been outlined above. The inadequacy of the current conception of the origin of resin canals has been demonstrated, and it is suggested that the pressure of secretion of resin may play an important part in the development of the resin-container. It should be emphasized that this is presented merely as a working hypothesis.

## THE EFFECT OF WOUNDING UPON THE PRODUCTION OF RESIN CANALS.

When the cambium of most conifers is injured, there is a great increase in the number of resin canals in the subsequently-formed secondary wood. The recent work of Thomson and Sifton has demonstrated that even the so-called "normal" or scattered resin canals in the wood of *Picea canadensis* can be traced to a cambial disturbance. This work suggests that traumaticism may have an importance, hitherto unsuspected, in causing the differentiation of resin-secreting tissue from the cambium. In view of these results, it seemed desirable to investigate the effect of wounding upon the production of primary resin canals.

A number of experiments were carried out in which growing points were subjected to wounds of varying severity; several types of material were used—growing root-tips of *Larix americana*, stems of *Pinus excelsa* and *P. sylvestris*, and young cotyledons of *P. pinea*. The wounds were effected by pinching with forceps, pricking with needles, etc., treatment which produced marked effects upon the cambium of these species. The wounds were labelled and left from June to September in most cases; then the material was collected and compared with unwounded controls. There were no significant differences in the presence and number of primary resin canals.

It seems that the canals of primary tissue are not induced by wounding, as is so strikingly the case in canals of the secondary wood. This difference in the effect of wounding may be more apparent than real. The secretion of resin takes place only within parenchymatous tissue. This is true even of the canals of the secondary wood; these often form a branching network of passages within a mass of parenchyma. In the experiments on growing points mentioned above, there was no abnormal development of parenchyma. Wounding of the cambium, on the other hand, causes an interruption in the differentiation of elements which would normally become tracheides; and so the effect of the wound is to increase the amount of parenchyma in the secondary wood, with a consequent increased secretion of resin.

This work was started at the University of Toronto, Canada, where innumerable kindnesses were shown by Prof. R. B. Thomson and Dr. H. B. Sifton, to whom I am deeply indebted. It was then continued at the Botany School, Cambridge, after the award of an Overseas Research Scholarship by the Royal Commissioners of the Exhibition of 1851, for which I offer grateful acknowledgment. Prof. A. C. Seward has supervised my work at Cambridge and has very kindly allowed me to use his library. I am also grateful to Mr. Tom Harris and Mr. A. K. Mitra for helpful criticism.

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## EXPLANATION OF PLATE 37.

Fig. 1. *Pinus Strobus.* Section of primary root showing large root-pole resin canals. (× 50.)

Fig. 2. *Pinus resinosa.* Section of lateral root with two root-pole canals, in one of which the lumen is almost closed. (× 80.)

Fig. 3. *Pinus excelsa.* Section of hypocotyl near the cotyledonary node. A horizontal canal ending in a bulb is shown leading from a root-pole canal. (× 80.)

Fig. 4. *Pinus excelsa.* Section of hypocotyl. The four root-pole canals are seen near their upper ends. Two canals in the secondary wood are also shown. (× 45.)

Fig. 5. *Pinus excelsa.* Section of epicotyl. (× 100.) For description see text, p. 622.

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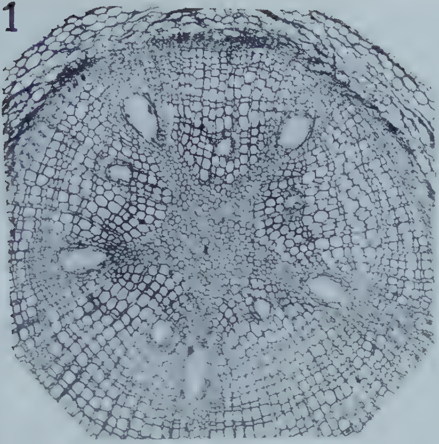

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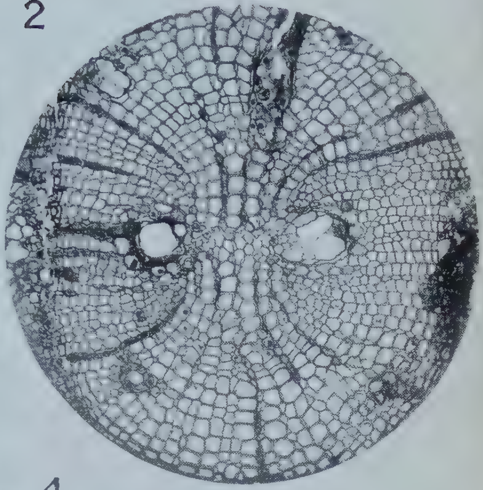

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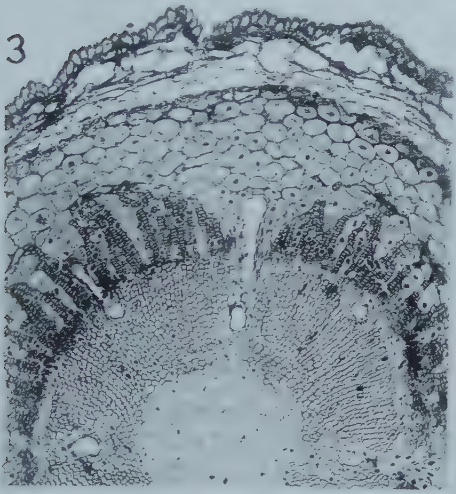

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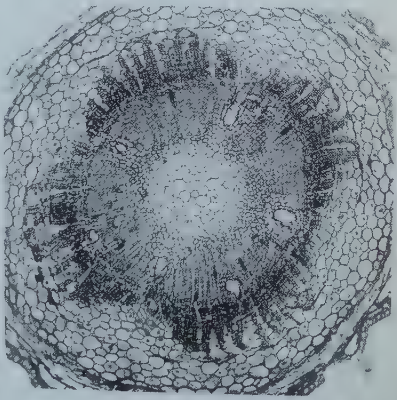

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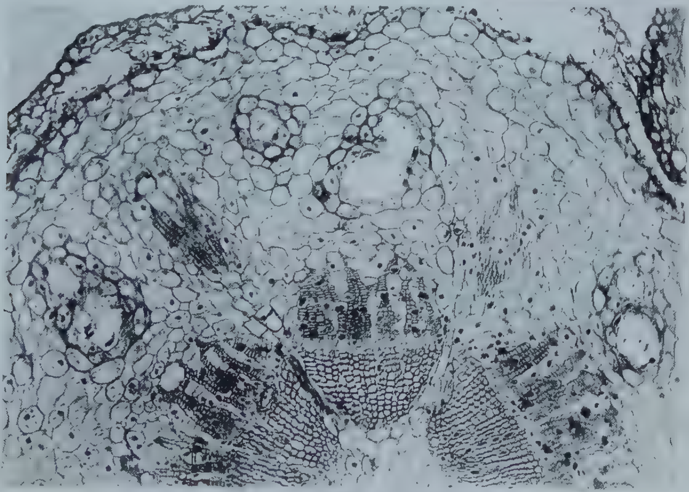

RESIN CANALS IN SEEDLING CONIFERS.

# HOOKER LECTURE.

## THE SWISS NATIONAL PARK.

(With PLATES 38-40.)

*THURSDAY, 15TH APRIL, 1926.*

By CARL SCHROETER, F.M.L.S.

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WITH great pleasure I have accepted the invitation to give the Hooker Lecture before the Linnean Society: in the first instance, because I have now the opportunity to thank you personally for the great honour you have bestowed upon me in electing me a Foreign Member of your Society. I am proud to be so closely connected with one of the most renowned biological societies of the world, and will try to show myself worthy of this distinction, which I owe more to the friendly feelings of my British friends than to my scientific merits.

Further, I am specially glad to speak in memory of Sir Joseph Hooker, for whom I have the greatest admiration. I admire him as one of the most successful systematists. That great work, the 'Genera Plantarum,' was possible only in Great Britain, where two men, using the unrivalled Kew Herbarium, were able to master the whole world of flowering plants. I admire him as one of the founders of modern Plant geography by his comprehensive studies on the Flora of New Zealand, Tasmania, and the Antarctic regions. I am sure that he would have taken a great interest in the subject of my lecture, because the studies in National Parks are destined to promote geobotanical problems.

I wish to speak about the biological researches in the Swiss National Park; but allow me to give first a short account of the Genesis, of the Ontogeny, so to speak, of our National Park. It is a part of the movement for the protection of Nature, which in Switzerland is becoming a great influence. Our Civil law permits even expropriation in the interest of natural and historical monuments, and many organisations are at work in this direction. Our numerous ornithological societies provide for the protection of birds in manifold ways; our society of foresters is interested in the conservation of interesting woods: our Liga für Heimatschutz protects the beauties of our landscape against disfigurement, and the Swiss Society of

Naturalists has created a special commission for the Protection of Nature, which has a subcommission in every single state of the Federation. The crown of the building is our "Naturschutzbund," the League for the Protection of Nature, which has now almost thirty thousand members paying an annual contribution of two francs, or fifty francs for life-membership. I would be very glad to be able to take back to Switzerland a long list of British Life-members, for the Conservation of Swiss nature is for the sake of mankind!

Let me sum up the results hitherto reached by these efforts. We have saved about four hundred erratic "blocs" from destruction; several times we have, together with the league for the conservation of scenery, protected mountains against profanation by railways—you will remember the danger menacing the Matterhorn! About fifty species of beautiful trees are reserved. Every canton has now its law for the protection of plants. About fifteen interesting fens and about twenty bird-asylums are being protected. Some asylums for marmots have been created, and the so-called free mountains, where shooting is forbidden, are also a valuable protection.

But the most effective, the most useful, the most durable measure was no doubt the creation of the Swiss National Park, situated in the Lower Engadine. It covers one hundred and forty square kilometres, equal to about fifty-four square miles. It contains the following parts:—

1. The central part—Val Cluozza, Tantermozza, Praspöl, Fuorn, and Stavelchod,—ninety-seven square kilometres, belonging to the parish of Zernez and taken on lease by the Government of Switzerland at a rent of twenty thousand francs; the leasehold is a sort of contract of service for ninety-nine years, which can be revoked only by the Government.

2. The western part—Val Trupchum, Muschauns, and Mela,—ten square kilometres, belonging to the parishes of Campovasto and Scanfs, taken on a lease of ninety-nine years.

3. The eastern part—the left flank of the valley of Scarl with the secondary valleys of Mingér, Foraz, and Tavru,—thirty-two square kilometres, belonging to the village of Schuls, which would lease only for twenty-five years. As the Government will take a lease only of ninety-nine years, it devolves on the Naturschutzbund to pay the rent of six thousand francs.

4. The intermediate part—Val Nüglia,—twelve and a half kilometres, belonging to the parish of Valcava, and taken on lease by the Government at a rent of eight hundred francs.

The following rules and regulations are in force for the whole Park. Human interference is absolutely excluded from the whole region. Shooting, fishing, manuring, grazing, mowing, and wood-cutting are entirely prohibited, no flower or twig may be gathered, no animal killed and no stone removed—even the fallen trees must remain untouched. In this way absolute protection is secured for scenery, plants, and animals: Nature alone is dominant. Anyone may visit the Park, but only simple alpine shelter-huts are provided, no hotels being allowed to be erected. Camping and the lighting of fires is prohibited. The custodianship of the Park is entrusted to four resident keepers.

The management of the whole is in the hands of five trustees, nominated by the Government. The State has further pledged itself to contribute a sum not exceeding thirty thousand francs per annum for the rent of the Park. The Swiss League for the Protection of Nature is bound to pay the cost of the construction and upkeep of paths and huts, equipment, and salary of the guardians, and scientific research in the Park. Moreover, the Swiss Society for the Advancement of Science is bound to organize these researches.

The district is peculiarly suitable for a National Park, for the following reasons. Its extension in both a horizontal and vertical direction is sufficient to ensure the reconstitution of a natural equilibrium; its mean elevation above sea-level is considerable, so that the snow-line lies as high as 3000 metres and the alpine tree-limit is at 2300 metres. Alpine life, therefore, can be widely developed in the area. In wildness and naturalness, as in loneliness and seclusion, it is scarcely surpassed anywhere in Switzerland. It is very sparsely populated, so that the prohibition of forestry and grazing operations involves but little hardship on its human population. It possesses extensive forests, of which the 2600 hectares of dense forest of erect mountain pine (*Pinus montana* var. *arborea*) deserve special mention. There are also magnificent forests of *Pinus Cembra*, mixed woods of spruce and larch (*Picea excelsa* and *Larix europæa*), a peculiar mountain race of Scotch fir (*Pinus sylvestris* var. *engadinensis*), and extensive areas occupied by the creeping mountain pine (*Pinus montana* var. *prostrata*). In addition to the great abundance of conifers, there is also a rich herbaceous flora, the great variety of geological substrata rendering possible the existence of both calcicole and calcifuge plants. The dividing-line between the floras of the western and eastern Alps passes through the region. In the National Park there is therefore a mingling of eastern and western forms, many eastern species, so far as Switzerland is concerned, appearing only in this district. Animal life, too, is abundant: chamois, marmots, deer, roes, foxes, mountain- and heath-cocks, golden eagle, etc., enlivening the landscape.

Even now, ten years after the beginning of reservation, the favourable effect is clearly visible: the flora of the now abandoned pastures has developed splendidly; we see real gardens of edelweiss, containing plants with fifty capita, and the number of animals has much increased—we counted for instance in 1918 twelve deer, in 1925 ninety. The roe has increased in the same time from sixty to one hundred and ninety, chamois from one thousand to twelve hundred and fifty, mountain-cock from ten to sixty, heath-cock from forty to one hundred and ninety, ptarmigan from one hundred and twenty to three hundred and ten, and golden eagle from fifteen to forty.

Some have criticised us for protecting beasts of prey, such as the fox and eagle; but we must not forget that these animals are exercising a very wholesome hygienic influence, as they kill the sick animals in the first instance! In a certain Bohemian district the foxes had been exterminated, and owing to this an epidemic disease of hares had so increased that foxes had to be reintroduced. We even hope that the bear, which has disappeared from Switzerland—the last bear was killed in 1904 in Val Mingér, in the National Park,—will make his reappearance.

The ibex, that splendid alpine animal, also disappeared from Switzerland in 1809, but there still exists a colony in the Italian Alps, in the Valley of Aosta. From this colony young animals have been brought to St. Gallen, where there exists now a flourishing colony. Also in Interlaken a colony of ibex has been established, and from these colonies we are now trying to reintroduce the ibex into our Alps, and up till now we have already four wild colonies, one of which is in the National Park. Its former existence there has been proved by old documents and by a skull found in the National Park.

For science the park represents an invaluable field for observation, unique because of the absolute exclusion of man's interference with the natural equilibrium. All the changes from the primitive state by the secular influence of shooting, fishing, woodcutting, cultivating, pasturing, grazing, haymaking, manuring will have to disappear gradually and the old primitive biocenose will have to be re-established. It is a grandiose experiment to create a wilderness.

It will be the principal task of scientific investigation to study all the successive stages of this return to the primitive stage. Of course, these studies must extend over a very long time. As a basis a complete catalogue of all living beings must be made and an intensive study of the biocenoses.

The successive changes will have to be investigated on a series of typical stations by means of exact analyses of the flora and fauna at long intervals, perhaps every twenty years, and, if possible, by means of photographs showing the different stages.

In this way the reclamation of pasture and meadows by the original forest may be studied, also the changes in animal life, the reaction of the flora of the pastures to the slowly diminishing manure and to the cessation of grazing and mowing. When the original condition has been eventually restored, we shall find if there were meadows originally in the forest region and which plants are truly original in the district; also the mode of immigration of forest in post-glacial time may be elucidated, and the tree-limit, which in our Alps has been lowered everywhere by human influence, will reach its climatic stand.

The absolute protection against disturbance by man or domestic animals makes our Park an invaluable natural laboratory for innumerable observations on the biology of plants and animals. A great mass of data, especially about animals, will be gathered by the daily observations of our guardians. Many investigations which otherwise would be subject to disturbance may be safely accomplished: for instance, on fructification when insects are excluded, parthenogenesis, hybridization, the effect of protection by snow, the longevity of perennial plants. By the work of successive generations of investigators it will be possible to follow up the truly natural successions and changes occurring within the area and to study the relations between soil, climate, and organism.

The Swiss Society for the Advancement of Science has enthusiastically undertaken the task of scientific investigation in the National Park, and in 1915 a special commission of fourteen members was elected. This has formed four sub-commissions: geographico-geological, climatological, botanical, and zoological. Detailed programmes for these investigations have been elaborated and quite an army of collaborators has been appointed. Until now no fewer than forty investigators have worked in the Park. Travelling expenses and maintenance are paid by the Naturschutzbund. The results are published in the 'Annals of the Swiss Society for the Advancement of Science.' Up to the present three zoological papers have been published and a botanical one is in print.

What, now, are the principal scientific results hitherto gained? Even before the reservation period the Lower Engadine and the Ofendistrict had been botanically explored. We have a Flora of the Lower Engadine by Killias, a geo-botanical Monograph of the Ofendistrict by Brunies, a paper on the Flora of the National Park by myself, and a very comprehensive report on an excursion in the Lower Engadine and in the National Park by Braun, with many sociological studies. The Lower Engadine belongs to the division of the Central Alpine pine valleys, characterised by a continental climate and many xerothermous plants. An interesting fact is the nonconformity of the immigration paths of the flora with the road of the valley: the most characteristic plants of the Lower Engadine have not come along the Inn, but from the southern valley of the Pintschgau over the pass of the Rechenscheideck.

The complete scientific investigation organised by our commission being still in progress, we can give here only the provisional results as published in the annual reports.

The meteorological subcommission under the presidency of the well-known Director of our central meteorological station, Dr. Maurer, has established three stations in the Park, at 1810, 1880, and 1950 metres above sea-level, with thermographs, sunshine recorders, and totalisator. The records show clearly the extreme continental character of the climate. There is a great difference between the extreme temperatures. For instance, the maximum at Buffalo is 23°·1 C., the minimum 33°·4 C.—a difference of 56°·5 C. The sky is quite Italian in its clearness: in 1922 we had 2000 hours of sunshine—almost as much as in our sunny Tessin, the "sunny verandah of Switzerland." Continental is also the very slight precipitation, 600 to 900 millimetres, our district being among the driest regions of the Swiss Alps.

The geographico-geological subcommission, directed by Prof. Chaix, from Geneva, has studied especially the interesting phenomenon of "block-glaciers," those wandering masses of blocks consisting of the moraines of dead glaciers, buried totally under the moraine shingle. The geological monograph of the district by Spitz and Dyrenfurth will be completed by our geologists.

The botanical subcommission under the direction of Prof. Wilczek, of Lausanne, has occupied thirteen collaborators with the following studies. The over-manured resting-places of cattle with their nitrophile vegetation have been analysed and photographed for the purpose of studying the changes in vegetation with the decrease of manure. Permanent quadrats have been laid in different associations in order to study the slow successions. All the associations of plants are studied by the sociological system of Dr. Braun-Blanquet, together with investigations on the soils, hydrogen ion concentration, contents of humus, and amount of calcium carbonate present. A paper now in print by Braun and Jenny on the alpine associations has shown very interesting results regarding the astonishing constancy of hydrogen ion concentration in the Curvuletum, the association dominated by *Carex curvula*. Also the progressive acidifying of soils has been demonstrated very clearly. The floristic exploration has led to the discovery of numerous new forms of plants—e. g., *Draba ladina* Braun-Blanquet, a new species of a group hitherto purely septentrional,—also a xerophytic variety of *Poa alpina* and several new mosses and liverworts.

The study of vertical distribution in connection with the continental climate has furnished many records of altitude—e. g., *Rhododendron ferrugineum* as high as 2840 m., and seven new plants for the snow region. Also many observations have been made on lichens, fungi, and algæ, and the microbes of the soils are studied quantitatively and qualitatively. A great many biological observations have been made, and the vernacular names in the localities have been studied because they often give interesting hints about former vegetation. A great many photographs of vegetation and habitats were taken in order to record the present state.

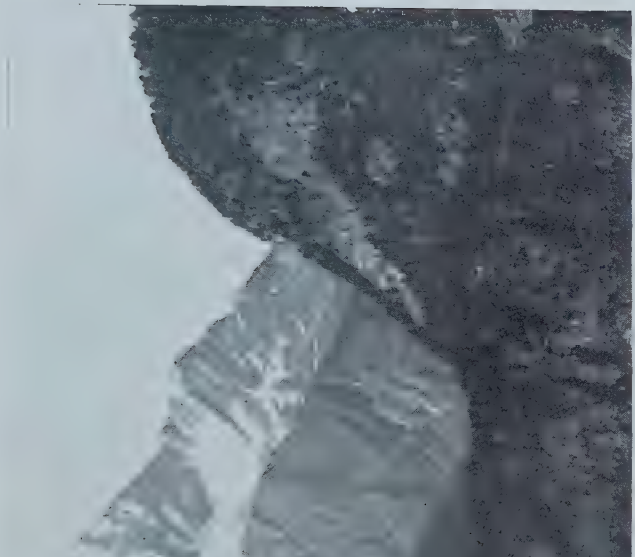
Our zoologists have published three papers: one, treating of the molluscs and referring to sixty-seven snails and mussels, particularly those inhabiting calcareous districts, as the primitive non-calcareous rocks are almost destitute of molluscs. The dryness of the climate seems responsible for the lack of large Helicides. As with plants, the main way of immigration of molluscs runs over the Rechenscheideck, and not along the Inn valley; seven species are Mediterranean and three (*Limax engadinensis*, *Campylæa rhætica*, and *Vertigo Zschokkei*, a new species) are endemic. Dr. Hofmänner has a paper on Hemiptera, listing one hundred and eighty-one bugs and thirty-six Cicadinæ and giving the same results as regards immigration. The Collembola, treated by Dr. Handschin, are represented by ninety-five species and twenty varieties. Thirty species are new to Switzerland and seven species and five varieties are new to science. The great number of high alpine and nival forms is surprising: fifty-two species, all endemic or boreal-alpine. The same author has found about 1400 species of Coleoptera, among these being twenty new species, all coming from the east. The Hymenoptera are also very numerous—for instance, not fewer than 350 species of Icheumonids have been found. Dr. Pictet, of Geneva, well known as a lepidopterist, has found many local races. The paths of immigration are different in this group from the others; they come briefly from the Münster valley and from the south, from Livigno along the valley of the Spöl. Dr. Barbey, a forester and a specialist on noxious insects, has given special attention to the question, whether the fallen decaying wood of the National Park, which is not removed, will become a danger to the neighbouring woods as a breeding-place of *Bostrychus*. He denies absolutely that there should be any apprehension on this score, adding that the primæval forest with its natural equilibrium suffers less from insects than does the cultivated forest. The game is studied by an experienced hunter, who states with pleasure the great number of young chamois.

There is good reason to believe that from the intense activity of our forty investigators we shall get eventually a complete idea of the inorganic and organic nature of our National Park. Three specially favourable conditions are to be mentioned: the absolute exclusion of human interference, the methodical collaboration of many observers, and the possibility of secular observations in this absolutely reserved area.

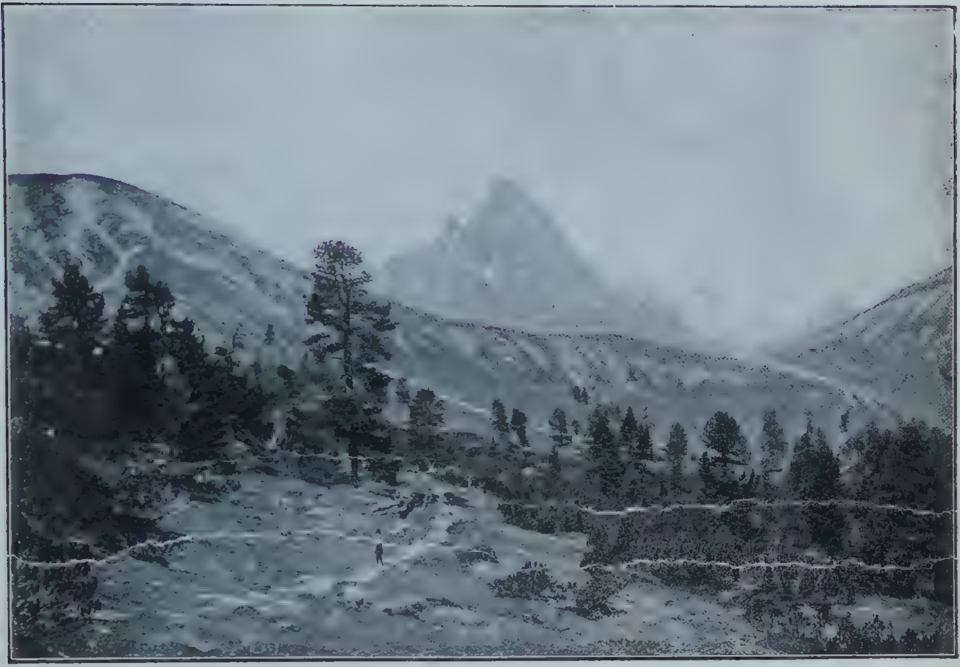
A trip through the Swiss National Park delights us not only by the wonderful scenery, by the wealth of Flora and Fauna, by the unique opportunity for scientific investigation, but also by the idea that a whole nation has solemnly taken a vow that here the whole must be preserved for all: that all personal advantage and all material profit are to be disregarded. A patriotic deed, the educational effect of which is very highly to be esteemed in our materialistic world.

Let me finish with the wish that I shall have at some time the very great pleasure of guiding a large party of members of your Society through our beautiful National Park.

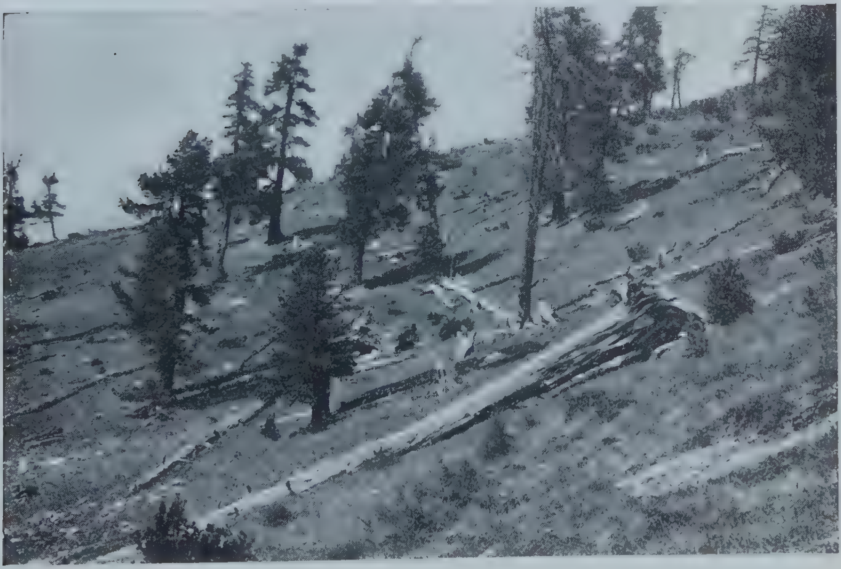
[The lecture was illustrated by over seventy coloured lantern-slides of the scenery, specimen trees, and alpine animals.]



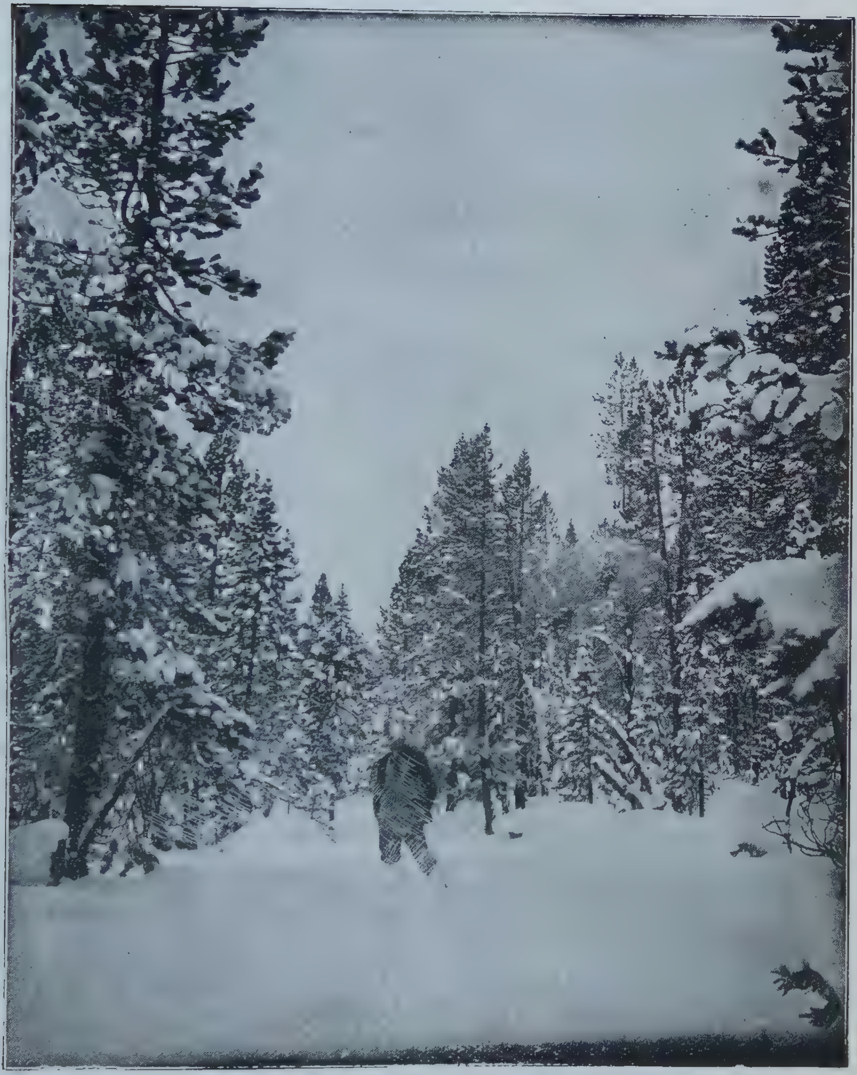
Piz Linard (3414 m.), the monarch of the Lower Engadine.



Val Mingér with Piz Plavna behind (3169 m.).
The conifers are *Pinus Cembra* and *Pinus montana* var. *prostrata*



The "fighting zone" (Kampfzone, "zone contestée" of de Candolle) between the limit of the dense forest and the timber-line, at Mount Caschera (*Larix europæa* and *Pinus Cembra*).



Forest of erect Mountain Pine (*Pinus montana* var. *arborea*).

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